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The Coralline Genus *Clathromorphum* Foslie emend. Adey

Biological, Physiological, and Ecological
Factors Controlling Carbonate Production
in an Arctic-Subarctic Climate Archive

*Walter H. Adey,
Jochen Halfar, and Branwen Williams*

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ABSTRACT

Adey, Walter H., Jochen Halfar, and Branwen Williams. The Coralline Genus *Clathromorphum* Foslie emend. Adey: Biological, Physiological, and Ecological Factors Controlling Carbonate Production in an Arctic-Subarctic Climate Archive. *Smithsonian Contributions to the Marine Sciences*, number 40, iv + 42 pages, 29 figures, 1 table, 2013.— The coralline algal genus *Clathromorphum* is a dominant calcifier in the rocky Subarctic biogeographic region, stretching through the lower Arctic from the Labrador Sea to the Bering Sea. Although commonly 2–10 cm in thickness, *Clathromorphum* can reach a thickness of up to 50 cm while forming an annually layered structure that can reach currently documented ages of up to 850 years. Geochemical and growth information archived in annual growth bands of *Clathromorphum* sp. has been used to provide long time series of past environmental conditions in regions that are poorly understood major drivers of Northern Hemisphere climate. However, information on *Clathromorphum* calcification, growth, and ecology that would allow interpretation of these records has previously been quite limited. Here we relate extensive field and laboratory data on the biology, physiology, and ecology of species of this genus and their controlling environmental parameters. We show that *Clathromorphum* has evolved a unique mode of double calcification, with high-magnesium calcite crystals, that enhances long life and leads to a multielement climate archive. Growth rates are controlled by temperature, and carbonate density is controlled by light, determined by both latitude and sea ice cover, whereas carbonate buildup and ultimate thickness are determined by local geomorphology and faunal interactions. Reproduction is complexly linked to vegetative anatomy. Precise paleoenvironmental information can be retrieved from *Clathromorphum* because of its unique cytological and anatomical structures, described and modeled for the first time in this volume.

Cover images: (left) One thousand year-old *Clathromorphum compactum* mound buried in a rhodolith bed (*Lithothamnion tophiforme*) in northern Labrador. Photo by Michael D. Fox; (center) Boulders at 25m depth heavily encrusted with *C. compactum* on the shore of low rocky island in northern Labrador. © Nick Caloyianis. Reprinted with permission; (right) Boulder with 200–300 year-old crust of *C. compactum* from southern Labrador. Coralline crusts on boulder sides are mostly *Lithothamnion spp.* © Nick Caloyianis. Reprinted with permission.

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The Coralline Genus *Clathromorphum* Foslie emend. Adey

Biological, Physiological, and Ecological Factors Controlling Carbonate Production in an Arctic-Subarctic Climate Archive

INTRODUCTION

Millennial understanding of past climate variability in the Subarctic and Arctic regions is crucial to prediction of the impacts of anthropogenic climate change both in the Northern Hemisphere and globally. In warmer latitudes, abundant tree ring and pollen data in the terrestrial environment and coral and bivalve data in the marine environment can provide data on past climates. However, considering the crucial role that sea ice, with its albedo effect, plays in controlling incoming solar energy, midlatitude data are inadequate to provide an understanding of global climate processes. Although recent studies have shown that encrusting coralline algae, abundant in shallow high-latitude seas, can record paleoclimatic information, considerable variation of unknown origin has provided conflicted analyses. In this volume we endeavor to show how an extensive field and laboratory effort directed at species of the coralline genus *Clathromorphum* can provide a detailed understanding of the complex biology, physiology, ecology, and habitat geomorphology of these species, which, in turn, can direct laboratory analysis and data interpretation.

THE SUBARCTIC SHALLOW BENTHOS AND COLD-WATER CARBONATES

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The Northern Hemisphere Subarctic region, as defined by the Thermogeographic Model, quantitatively demonstrated with crustose corallines (Adey and Steneck, 2001), and further supported by quantitative analyses of benthic seaweeds (Adey and Hayek, 2011), stretches from the northwestern North Pacific to the northwestern North Atlantic. Many benthic species that characterize the Subarctic occur in both Pacific and Atlantic segments of the region (Olsen et al., 2004; Adey et al., 2008), although the separated populations tend to be genetically distinct (Addison and Hart, 2005; Coyer et al., 2006). Relatively few species are endemic to the North Atlantic Subarctic, whereas many species are endemic to the considerably larger North Pacific Subarctic (Briggs, 2003). The Arctic has very few endemic genera and only a small number of species; it is dominated by Subarctic species (Adey et al., 2008).

Wherever rocky bottom occurs in the sublittoral Subarctic (typically to 40 m, depending upon exposure and salinity), it is irregularly coated by an extensive but patchily discontinuous crust of biogenic calcium. This carbonate crust (typically 0.5–10 cm thick, but to over 0.5 m in thickness; Lebednik, 1976) is present on all but the most mobile or friable rock surfaces (Frantz et al., 2005; Adey and Hayek, 2011). Because it is a high-magnesium carbonate, laid down mostly by coralline red algae, this crust can be called a cor-strome. It also occurs in the Arctic, where it is built largely by Subarctic coralline species (specimens and images in the U.S. National Herbarium); however, its continuity is unknown. The depth zone immediately below the cor-strome, where broken fragments accumulate and some species of *Lithothamnion* continue to grow in the mobile state as rhodoliths, has received some attention (Freiwald and Heinrich, 1994), but the cor-strome itself remains largely unstudied.

In both the Atlantic and the Pacific, these carbonate-encrusted bottoms have been widely referred to as “coralline, sea urchin barrens” (Mathieson et al., 1991; Estes and Duggins, 1995; Steneck et al., 2002); however, this description is certainly a misnomer, as they may well be among the richer shallow marine bottoms of the marine Holarctic (Himmelman, 1991; Chenelot et al., 2011). The Chenelot et al. (2011) study focused on abundant invertebrates resident in *Clathromorphum nereostratum* in the Aleutian Islands, but it is likely that a similar relationship exists for cor-stromes in the northwestern North Atlantic. Drying fragments of cor-strome on research vessel laboratory benches generally release large quantities of invertebrates, especially grazing chitons and filter-feeding brittle stars. A Labrador fjord *Lithothamnion glaciale* cor-strome produced 740 macro-invertebrates from 637 cm² of crust (Adey, unpublished field notes). Thus, there is little question of the coral reef-like richness of these bottoms; what is lacking is geographically widespread quantitative research on invertebrate diversity and biomass.

Considerable debate exists concerning the primary ecological drivers of ecological structure on Subarctic-Boreal rocky bottoms (e.g., Steneck et al., 2002; Springer and Estes, 2003; Estes et al., 2005; Trites et al., 2007); is it climate, top predators, overfishing, or some complex of the three that drives the major fluctuations of the associated kelp beds observed over the last half century? These issues carry special weight because of the collapse of numerous major cold-water fisheries over the last several decades, the currently expanding Arctic fisheries, and the ongoing debate over climate change and its causes. Much of this debate has focused on the Bering Sea and Aleutian Islands and the Gulf of Maine and Nova Scotia. However, the carbonate bottom, with the rich diversity it harbors, has been considered at best a backdrop in the debate over large seaweeds, grazing invertebrates, and sea mammals and at worst a “barren” created by imbalances among the major, large players. As we will discuss at depth, the age of the cor-strome frequently reaches one to three centuries, and the maximum age of specimens now under study exceeds 800 years in the Aleutian Islands and 600 years in the Labrador Sea. The biological constant in these regions of

scientific dispute, a basal calcified coralline crust with centuries of growth, is the least studied element.

Several species each of the genera *Clathromorphum*, *Lithothamnion*, and *Leptophytum* are the dominant producers of the Subarctic-Arctic cor-strome. In the fully Subarctic northwestern North Atlantic, *Clathromorphum compactum* is an abundant species encrusting rocky bottoms in the mid-photic zone (10–20 m; Adey, 1966b), being largely replaced by *Clathromorphum circumscripum* in shallower waters and *Lithothamnion glaciale* in deeper waters. *Lithothamnion glaciale* also tends to replace *C. compactum* as the dominant cor-strome producer in inner bays and fjords, where siltier and fresher waters usually dominate. In many localities, depressions within the rocky cor-strome bottoms are filled with mobile nodules (rhodoliths) largely derived from fragments fractured from the *Lithothamnion* cor-strome by waves and bioturbation. Extending below the rocky cor-strome and continuing to significant depths (20–60 m), beds of rhodoliths, usually as part of a shelly gravel substrate, are widespread. However, the full extent of these beds is poorly known. Two species of *Lithothamnion* (*L. glaciale* and *L. tophiforme*) are the dominant producers of rhodoliths, the former species being more Subarctic and the latter more Arctic (Adey et al., 2005).

As previous studies have demonstrated (Halfar et al., 2007, 2008, 2011a; Frantz et al., 2005; Hetzinger et al., 2011; Williams et al., 2011), these centuries-old carbonate formations, through analysis of their temperature- and light-dependent growth layers and the trace chemical structure of their carbonate cell walls, can provide significant climate archives. The coralline provides a surface for algal epiphytes, and both the corallines and the epiphytes are grazed by many invertebrates. They are also very important producers of secondary biomass, mostly by providing a porous, reef-like habitat to innumerable invertebrates that utilize mostly planktonic sources of primary production (Chenelot et al., 2011). Additionally, they provide significant ecosystem support for Subarctic-Arctic fisheries that are now expanding in importance. These key Arctic and Subarctic ecosystems have a detailed history written into their basal biogenic carbonate; to read this history, we need only to extract the Rosetta stone of anatomical and geochemical information.

THE DISTRIBUTION OF *CLATHROMORPHUM* SPECIES

Although a few species of the genus *Clathromorphum* have been described for the colder Southern Hemisphere (<http://www.algaebase.org>), their relationship to the abundant Northern Hemisphere species is currently uncertain. In the Northern Hemisphere, the four epilithic species are largely restricted to the Subarctic and Arctic or its fringes, including the Aleutian Islands (Lebednik, 1976). Two additional species, *C. parcum* and *C. reclinatum*, are obligate epiphytes with limited archival value, and we will not discuss them further; phylogenetic studies currently underway (Adey et al., unpublished) show that these two species belong to a different clade. They are Boreal and fringe Subarctic in distribution only in the North Pacific.

Clathromorphum circumscriptum is the most widely distributed member of the genus, ranging from Hokkaido, Japan, and British Columbia (Adey et al., 1976; Lebednik, 1976) in the North Pacific through the Arctic to the southern Gulf of Maine in the western Atlantic and Iceland and the Norwegian fjords south to Trondheimsfjord (Adey, 1965, 1971) in the eastern Atlantic. Restricted largely to intertidal pools and the shallow sublittoral, *C. circumscriptum* can (rarely) achieve 5–10 cm in thickness. However, both the conceptacles and the intraconceptacle vegetative crust in this species always break out at reproductive maturity, considerably disrupting thallus layering. Together with a tendency to experience greater environmental disturbance, it is a possible, but generally poor, subject for climate archiving.

Clathromorphum compactum, a cold-water carbonate builder and a primary subject of this volume, extends from northeastern Hokkaido, Japan, through the Arctic to the central Gulf of Maine in the western Atlantic (Adey et al., 2008) (Figure 1). *Clathromorphum compactum* is not reliably known from Iceland or Norway, occurs in deeper water, and is conspicuously more limited to colder water than *C. circumscriptum* (Adey, 1965; Adey et al., 1976). Adey et al. (2008) treated *C. compactum* as

an Arctic species, although it is more likely Subarctic in origin and distribution. Although collection sites in the Arctic are only scattered, *Clathromorphum compactum* is generally an abundant species wherever it is found, and rock substrate, coastal salinity, and a high sediment load are not limiting.

Clathromorphum nereostratum (Figure 1) and *Clathromorphum loculosum* are cor-strome formers and appear to be largely restricted to the Aleutian Islands; both species are reported for the Asian mainland coasts, but insufficient definitive work has been carried out in the Okhotsk and western Bering Seas to determine whether they are significant components of the algal flora. *Clathromorphum loculosum* has a leafier growth morphology (Lebednik, 1976), and its archival potential is unknown. *Clathromorphum nereostratum* is the most massive of the *Clathromorphum* species, largely because of its Subarctic-Boreal fringe environment in the Aleutian Islands. *Clathromorphum nereostratum* and *C. compactum* are conspicuously layered, often with buried conceptacles, and provide the greatest opportunities for climate archiving. Both the Arctic and the northeastern Asian mainland and its off-lying islands provide a largely unknown and potentially rich region for cor-strome climate archiving. Here we

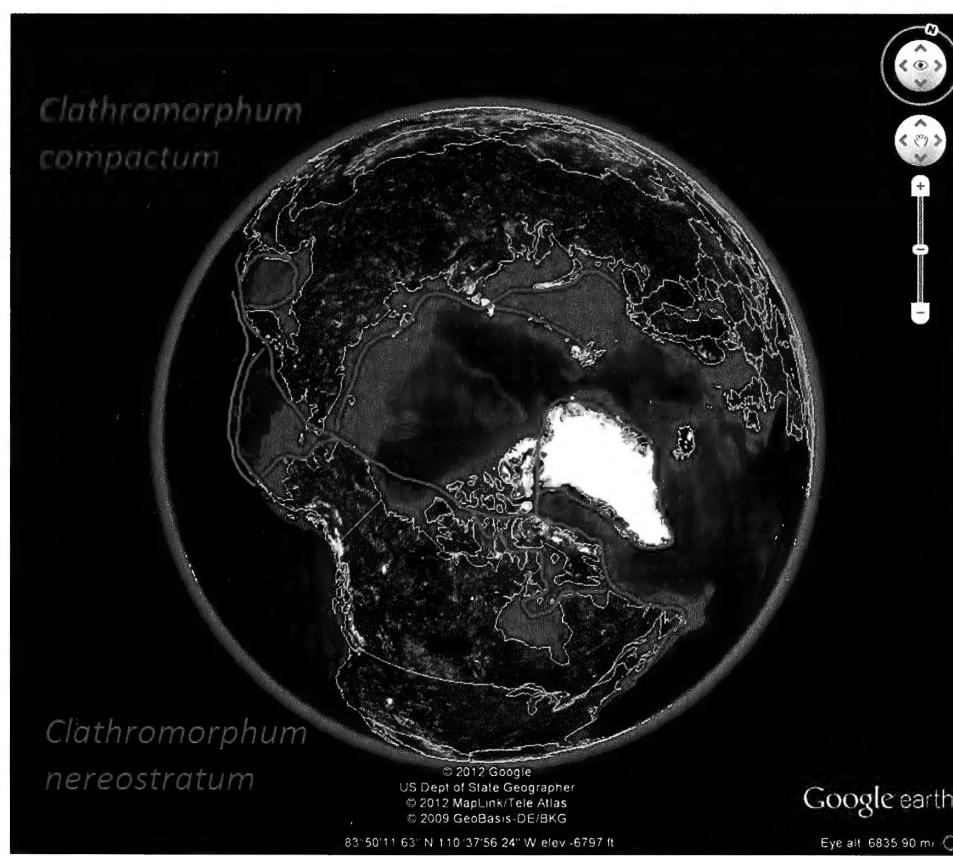


FIGURE 1. Known geographic distribution of principal *Clathromorphum* clathrostrome formers. *Clathromorphum nereostratum* has been reported from the mainland coast of easternmost Asia, but records need to be verified.



FIGURE 2A. *Clathromorphum compactum* buildup (clathrostrome) crowning large cobble in cor-strome, including branching *Lithothamnion* spp. at 20 m depth in southern Labrador. Crusts are 2–4 cm thick and 100–250 years old. Green sea urchins (*Strongylocentrotus droebachianus*) are 30–50 mm in diameter. © Nick Caloyianis. Reprinted with permission.

introduce the term clathrostrome to refer to extensive carbonate crustal buildups dominated by the two *Clathromorphum* species, *C. compactum* and *C. nereostratum*.

BIOLOGY AND ECOLOGY OF CLATHROMORPHUM

As with most red algae, crustose corallines have a basic filamentous structure; in this group, the filaments are fused into a calcified crust (Figures 2A–2C). As described by Adey (1964, 1965, 1966a, 1966b) and Adey et al. (1982; 2005), crustose corallines combine these filaments into complex tissues with the filaments linked by fusions and/or secondary pits. Also, several different patterns of growth, within the carbonate framework, characterize different genera (Adey et al., 2005). In many cases the development of reproductive structures occurs within perithallial tissue and is integrated with the growth of that tissue. Given damage to the overlying meristem or in the formation of conceptacle fertile discs, meristematic activity can be reinitiated

within the uppermost years of perithallial tissue (forming characteristic wound repair tissue).

Like many higher plants and unlike all other red algae, corallines have an intercalary meristem (Adey, 1964; Adey et al., 2005; Figure 2C); along with other elements of their anatomy and reproduction, this characteristic has led to their separation as an order of red algae (Corallinales; Silva and Johansen, 2007). Recent phylogenetic work suggests the group may be separable at the level of subclass on the basis of the structure of cell pit connections (Bittner et al., 2011). In a multigene analysis of genera with multipored conceptacles, currently under development with colleagues (Adey et al., unpublished), we are able to show that *Clathromorphum* forms a distinct clade most closely related to *Leptophytum* and distant from the *Lithothamnion* and *Phymatolithon* clades.

Corallines occurring on hard bottoms in shallow seas can be reef formers in the tropics (Adey, 1998) and rock-blanketing carbonate formers (cor-stromes) in colder waters. They are often

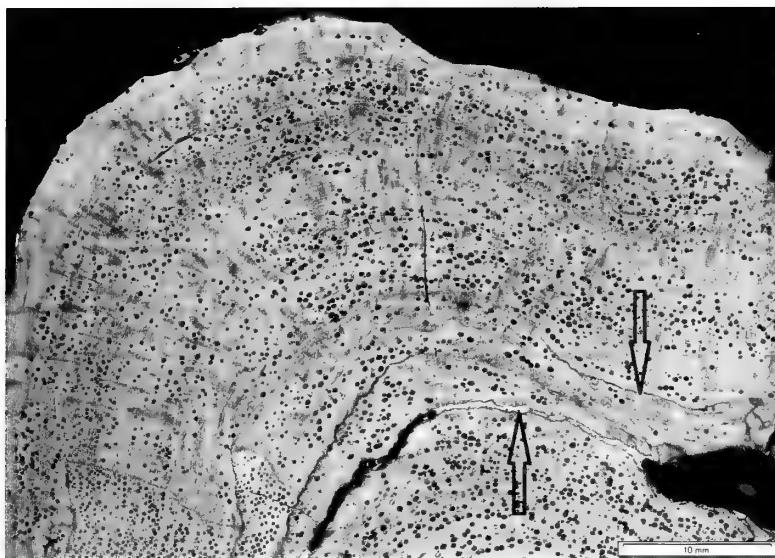


FIGURE 2B. Polished section of 4-cm-thick, 220-year old mound of *C. compactum* (same locality as Figure 2A). Note distinctive yearly banding, variably abundant conceptacles (ovoid holes), and large unconformity near the base of the specimen (up arrow). Partial unconformities are scattered throughout crust (down arrow).

fossilized and have been used as paleoecological indicators from the early Tertiary (Adey, 1979). Coralline growth is slow; yearly bands in *Clathromorphum* in the warmer fringes of the Subarctic and the Aleutian Islands are 300–400 µm in thickness. In the colder Subarctic, the principal habitat of *C. compactum*, they are considerably thinner and drop below 100 µm yr⁻¹ in the Arctic. Although the potential for climate archiving with corallines has been known since the 1960s (Adey, 1965; Chave and Wheeler, 1965), its application has been frustrated until recently by a lack of understanding of their anatomical complexity and its irregularities, as well as by the lack of appropriate instrumental tools.

Species of *Clathromorphum* have a unique anatomy that is particularly useful in the development of climate archives in Subarctic marine environments (Adey, 1965; Halfar et al., 2011a). Unlike the progressive cell growth in other Subarctic corallines, where maximum cell length is achieved several to a dozen cells below the meristem, creating a diffuse, time-delayed band of calcifying cells, *Clathromorphum* produces all of its growth and calcification in the meristem cell layer (a cambium analog; Adey et al., 2005; Figure 2C). As shown here, in *Clathromorphum* the band of calcification and growth is even narrower than meristem cell length, occurring on a plane a few microns thick passing laterally through the meristem; this ensures the tight temporal linking of ambient water climate and chemistry to a narrow plane of calcite crystals. These species have an intricate anatomy that includes calcite crystals that preserve, in their trace element and isotopic structure, an array of environmental proxies.

In addition to their carbonate skeleton, species of *Clathromorphum* have evolved partial protection against grazing by invertebrates in both their anatomy (the sunken meristem) and their primary asexual reproduction (conceptacles are sunken in the crust and produced in winter). Working with *Clathromorphum circumscripum*, Steneck (1982) demonstrated a “co-evolved interdependency” with the limpet *Acmaea testudinalis*.

Removal of epithallial surface cells by limpets during grazing equaled the production rate of epithallial cells in the meristem while freeing the surface of epiphytes. The same relationship likely exists for *C. compactum* and *C. nereostratum*, as fine grazing marks are abundant on the surface of most collected specimens (in most of the Subarctic, the chiton genera *Tonicella* and *Ischnochiton* dominate). Since routine grazing by chitons and limpets is concentrated on the upper surface of the epithallium, the perithallium, which builds cell-by-cell below the meristem,

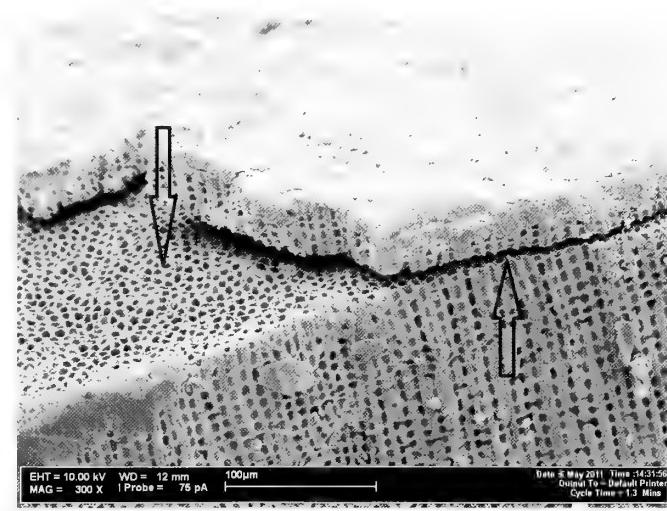


FIGURE 2C. SEM image of fractured *C. compactum* mound. The lower right face (right arrow) shows calcified perithallium filaments. The upper thin slab breaking off is epithallium. The exposed surface to the left (left arrow) is meristem, separated through the middle of the layer at the plane of growth and calcification.

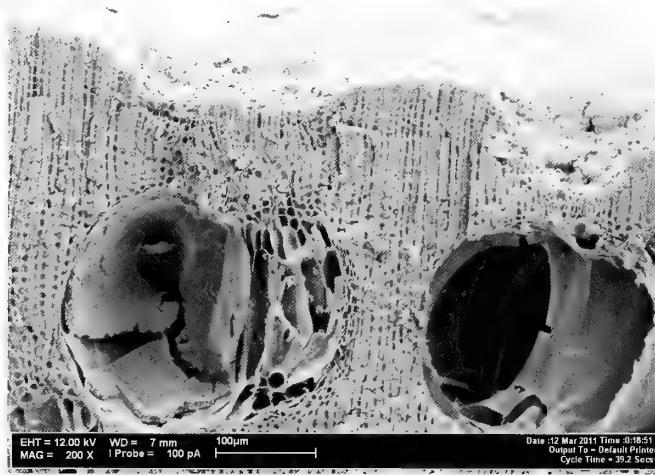


FIGURE 2D. Vertical fracture of *C. compactum* from southern Labrador with late mature asexual (multipored) conceptacles. The conceptacle to the right shows a roof and sporangial pore, exposed by the breakout of the conceptacle cap (epithallial plug overlying developing conceptacles). The roof of the postmature conceptacle to the left is growing in with new meristem.

can provide an archive of water climate that is often undisturbed for centuries by grazers or other organisms.

Most corallines form reproductive structures in peripherally uncalcified packets, called conceptacles, which can be scattered or densely arrayed across the crust surface; conceptacles are integral with perithallial tissue but can either be buried below the surface or protuberant above the crust surface. Patterns of origin and development, relative to the perithallial tissue, vary widely between genera. In some genera, conceptacles originate deep within the perithallium, sloughing off caps of overlying perithallial carbonate at maturity (e.g., *Phymatolithon* and *Leptophytum*; Adey, 1964, 1966a). In *Clathromorphum* conceptacles originate in the meristem, develop upward, as allowed by the growth of the surrounding vegetative tissue, and remain buried in that carbonate-encasing tissue at least until maturity (Adey, 1965). Some species of *Clathromorphum*, including *C. compactum* and *C. nereostratum*, bury their conceptacles with continued growth; successive years leave layers of conceptacle “holes” in the crust that document seasonality (Figures 2B, 2D, 2E). The principal *Clathromorphum* species with archival value initiate conceptacle development in the early autumn, apparently regardless of latitude. In the later stages of conceptacle maturation, to make room for the enlarging sporangia, the calcite in the immediately surrounding tissue is first dissolved, and then the remaining organic tissues are crushed by the enlarging sporangia; roughly 30%–50% of a conceptacle cavity’s height and 50% of its width result from this crushing.

CALCIFICATION

The skeletal carbonate in corallines forms as prismatic high-magnesium calcite crystals, perpendicular to the filament axis, within the organic wall of each cell (Adey, 1998). In most coralline genera, a thin layer of tabular crystals forms between the individual filaments and serves as a “glide plane,” allowing differential cellular extension (growth; Adey et al., 2005). *Clathromorphum* species lack differential cellular growth and have a very different mode of calcification, which we will describe in detail below. In the Subarctic and its fringes, some *Clathromorphum* species can be very long-lived (at least many centuries). Given favorable environmental and geomorphological circumstances, *C. compactum* and *C. nereostratum* can build crusts with a substantial thickness of biogenic, high-magnesium carbonate (Figures 2B, 2F). With the convergence of an enhanced understanding of species ecology and preservational geomorphology, multiple complementary analytical techniques, and a full understanding of cellular anatomy, limitations to the climate archive potential of these species are finally being overcome.

THE NEED FOR AN ARCTIC-SUBARCTIC ARCHIVE

Much of the climate variability in the North Atlantic is dictated by the North Atlantic Oscillation (NAO), which is a hemispheric meridional oscillation in atmospheric mass with centers near Iceland (low) and over the subtropical Atlantic (high; Hurrell, 1995). However, the Labrador Sea and its coastal currents (the West Greenland Current and the Labrador Current) function somewhat independently of the NAO. Variability in North Atlantic Deep Water formation in the Labrador Sea impacts both the global Thermohaline Circulation and the cold and relatively fresh Labrador Current (Drinkwater and Mountain, 1997; Colbourne, 2004). Future climate predictions depend on a clear understanding, reaching back many centuries, of the relationships among the dominant climate parameters: the NAO, water temperature and salinity, the North Atlantic Deep Water formation, and Labrador Current mass transport.

The main branch of the Labrador Current flows along the edge of the Labrador and Newfoundland shelf (Lazier and Wright, 1993), whereas an inshore branch follows the various cross-shelf saddles and inshore troughs (Colbourne, 2004). Rapid climate changes beginning in the late 1980s produced an enhanced outflow of low-salinity waters from the Arctic and a general freshening of the Labrador Current (Greene and Pershing, 2007). Recent and substantial evidence for rapid changes in North Atlantic climate include increased Arctic air temperatures (Thompson and Wallace, 1998), decreased sea ice extent (Comiso, 2006), record minimum sea ice (Gersonde and Vernal, 2013), increased melting of the Greenland ice sheet, and freshening of the North Atlantic (Curry and Mauritzen, 2005). Understanding the mechanisms responsible for the recently observed changes in the strength of the Labrador Current and climate variability in the subarctic Atlantic requires analysis of long climate time series (Sutton and Hodson, 2003).

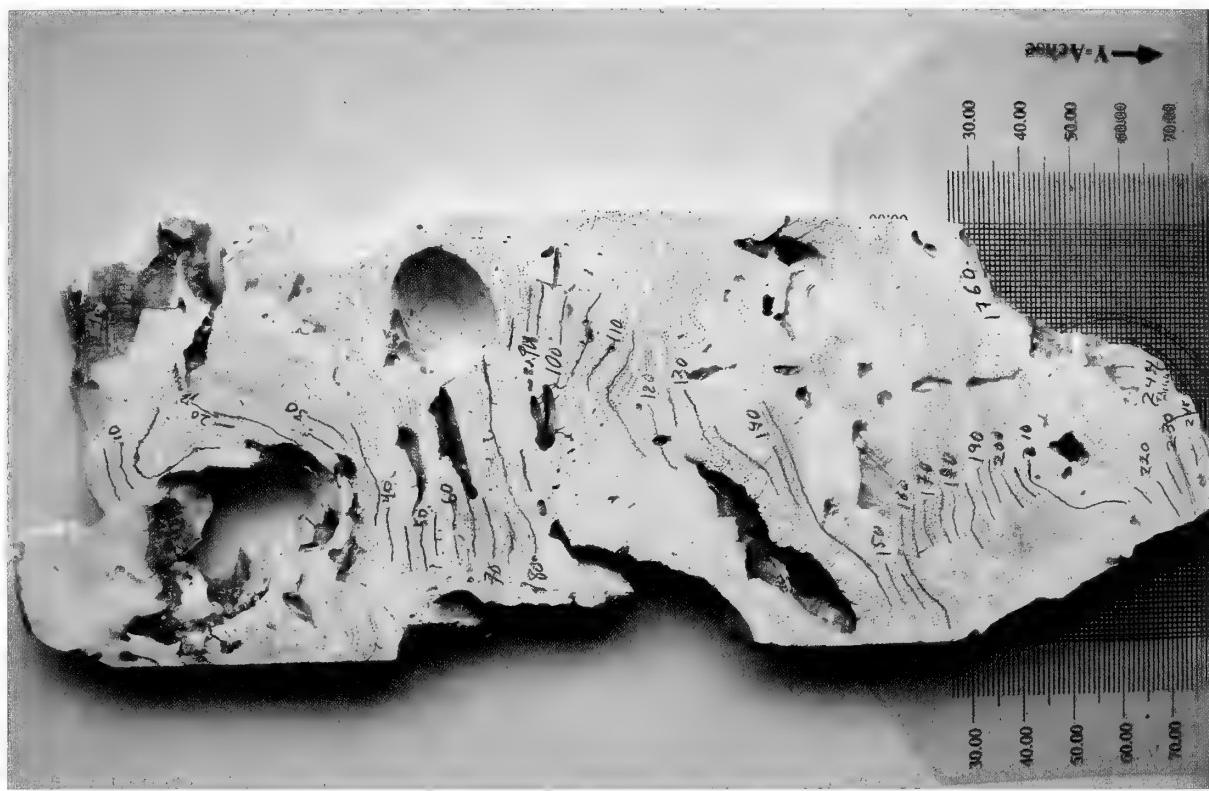


FIGURE 2E. Polished slab of *C. nereostratum* from the Aleutian Islands, showing 244 years of growth.



FIGURE 2F. *Clathromorphum nereostratum* from the Aleutian Islands. At 20 cm thick, the crust is over 400 years old.

Likewise, a millennial understanding of past ocean climate variability in the North Pacific–Bering Sea region is crucial to the prediction of the impacts of anthropogenic climate change on this rich ecosystem and on the role played by this region in Northern Hemisphere climate at large. Links between the North Pacific and North Atlantic climates clearly exist, but they are poorly understood (Hetzinger et al., 2012). The Bering Sea, a region transitional between Arctic, Subarctic, and Boreal regions in the North Pacific (Adey and Hayek, 2011), is particularly sensitive to warming because of its seasonal ice cover (Sigler, 2010); continuation of the warming trend of the past decade (Overland and Stabeno, 2004) will have a major impact on its fisheries and seabird and marine mammal populations (Grebmeier et al., 2006). As in the Labrador Sea, limited instrumental climate data for the North Pacific and Bering Sea are available, only from 1900; significant sea surface temperature (SST) information is available only from the mid-1950s (Hetzinger et al., 2012).

At present, sclerochronological analyses of the bivalve mollusk *Arctica islandica* provide the bulk of annual- to subannual-resolution paleoclimate data for near-surface waters in the northwestern North Atlantic (Wanamaker et al., 2008, 2011). However, the northernmost confirmed occurrences of *A. islandica* are found along the southern shore of Newfoundland (Dahlgren et al., 2000), which is the southern boundary of the core Subarctic. Limited paleoproxy archives exist for the North Pacific, but most high-resolution climate reconstructions are inferred from tree ring chronologies and do not provide oceanic SST patterns (Hetzinger et al., 2011). Recent studies have shown that encrusting coralline algae are high-quality recorders of extratropical paleoclimatic signals because of their (1) abundance in mid- to high-latitude oceans, (2) multicentury life span (Halfar et al., 2011a), and (3) annual incremental growth patterns in a high-Mg calcite framework that can be targeted for high-resolution geochemical sampling (Halfar et al., 2007; Williams et al., 2011).

Clathromorphum has an intricate anatomy and reproduction; the climate history of the late Holocene is written in its yearly banding and calcite crystals. This study demonstrates how an understanding of the biology, physiology, ecology, and habitat geomorphology of two principal species of this genus is essential to the further development of a high-resolution climate archive for the Arctic and Subarctic. Reading this climate archive requires not only an intimate knowledge of the interactions between climate and the complex linkages among the reproduction, growth, anatomy, and ecology of these two species but also high-resolution analytical techniques that reveal the underlying structural details that are the outcome of these interactions.

CORALLINES AS CLIMATE PROXIES

Mg/Ca Ratios and Seawater Temperature

The magnesium content of coralline algal skeletons records temperature changes (Figures 3, 4; Adey, 1965; Chave and Wheeler, 1965). Such records have been greatly expanded (Hetzinger et al., 2009, 2011; Gamboa et al., 2010; Kamenos, 2011)

using laser ablation–inductively coupled plasma–mass spectrometry and electron microprobe analyses. Research currently underway is producing data covering multicentury time scales.

Ba/Ca Ratios and Salinity

The barium content of the calcium carbonate skeletons of several marine calcifiers has served as a proxy for identifying changes in the mixing of cold, nutrient-rich deep waters at the surface (Lea et al., 1989; Fallon et al., 1999) or as a tracer for riverine inputs. Chan et al. (2011) have shown that changes in the Ba/Ca ratio in *Clathromorphum* indicate freshwater-induced changes in ocean stratification. Analyses of this ratio provide a proxy for assessment of salinity changes resulting from meltwater introduced into the Gulf of Alaska and the Alaskan Coastal Current, as well as being an important source of information on freshwater delivery into the Arctic Ocean.

Growth as a Climate Archive

A 115-year growth record from specimens of *C. compactum* from Newfoundland and Quebec (Figure 5) produced a century-long proxy archive for temperature in the northwest Atlantic (Halfar et al., 2011b). This chronology was successfully compared to climate patterns of the Atlantic Multidecadal Oscillation. Halfar et al. (2011a) linked information from yearly band widths with cloud cover related to the Aleutian low-pressure system. Combined with Mg as a proxy for temperature, a 640-year record of annual growth for *C. compactum* in the Labrador Sea has been correlated with sea ice cover (Halfar et al., unpublished manuscript).

Isotopic Composition

The oxygen isotope composition in the skeletons of *Clathromorphum* species records ambient seawater temperature. Similarly, the high-magnesium carbonate content of these species records $\delta^{13}\text{C}$ values from the dissolved inorganic carbon in the surrounding seawater. Williams et al. (2011) measured $\delta^{13}\text{C}$ in the coralline alga *C. nereostratum* to reconstruct the entry of anthropogenic CO_2 into the northern North Pacific Ocean and Bering Sea (Figure 6). From 1887 to 2003, the average decadal rate of decline in $\delta^{13}\text{C}$ values increased from 0.03‰ yr^{-1} in the 1960s to 0.095‰ yr^{-1} in the 1990s; this result is higher than expected from the $\delta^{13}\text{C}$ Suess effect. The authors concluded that an increasing intensity of the Aleutian atmospheric low was responsible for the upwelling of carbon-rich deep water.

MATERIALS AND METHODS

The collections utilized in this study were taken on scuba dives based from small research vessels, which allowed bottom surveys and assessments of the ecology and geomorphological characteristics of cor-stromes. The research vessels were equipped with laboratory facilities that allowed microscopic examination

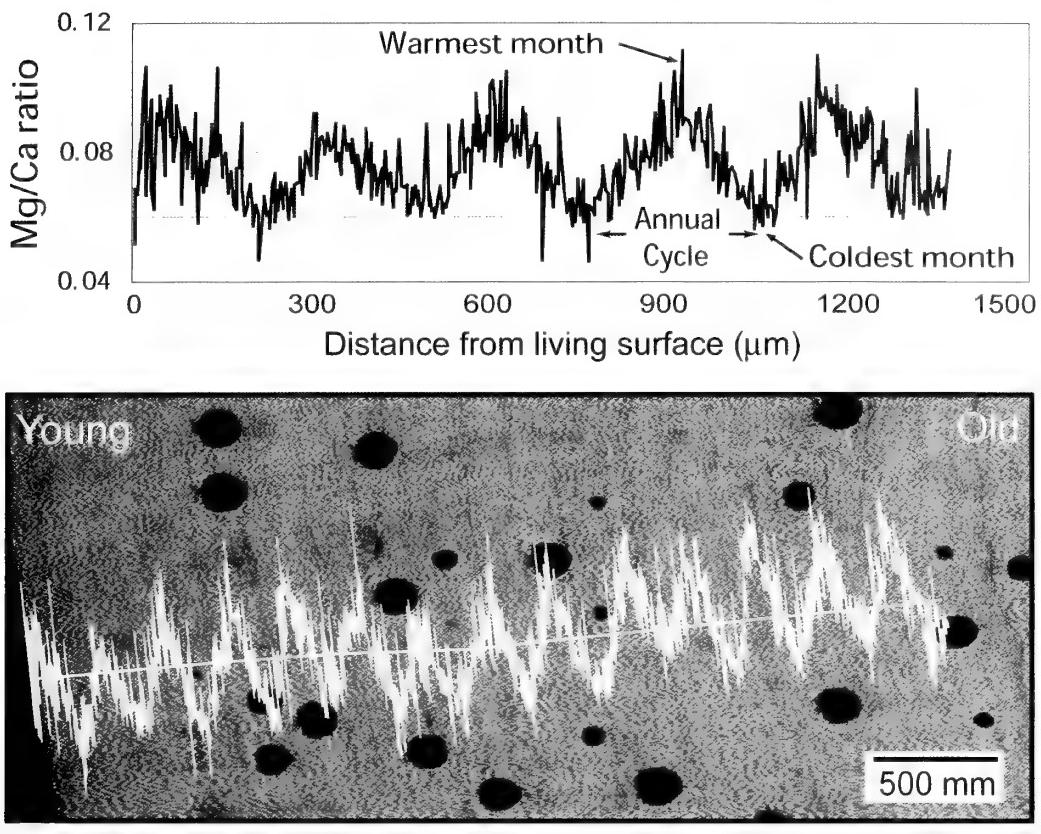


FIGURE 3. (top) Annual Mg/Ca cycles (moles) measured by laser ablation–inductively coupled plasma–mass spectrometry. (bottom) Mg/Ca cycles superimposed on a cross-section view of *C. compactum*. The white line laser transect is along the growth axis (Halfar et al., 2011a).

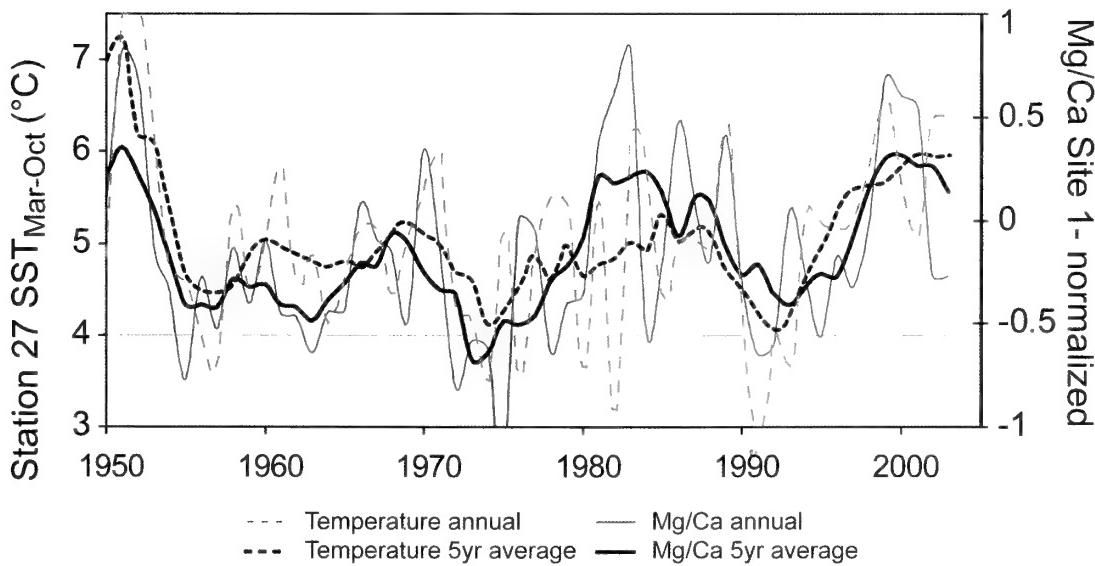


FIGURE 4. Mg/Ca time series from *C. compactum* near St. Johns, Newfoundland (average of two samples), and instrumental temperatures at a nearby oceanographic station (station 27.0 m depth; 1950–2004); $r_{\text{annual}} = 0.51$, $p < 0.001$ (Gamboa et al., 2010).

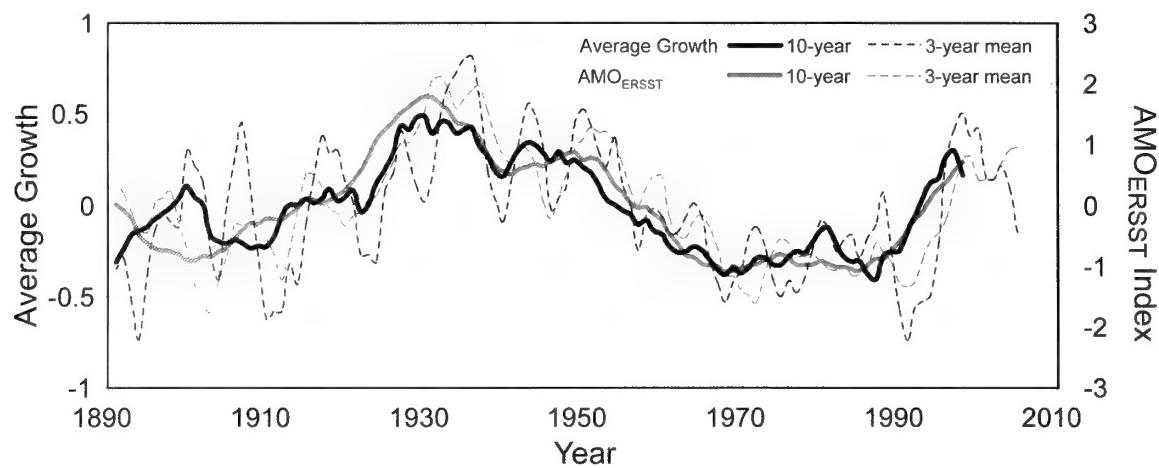


FIGURE 5. Ten-year moving average of 115-year growth increments; master chronology of Newfoundland *C. compactum* compared to the Atlantic Multidecadal Oscillation (AMO; $r = 0.74$; Halfar et al., 2011a).

and specimen labeling, drying, and initial measurement. Extractions from rocky bottoms were mostly made manually, with a hammer and chisel; although 10%–20% of specimens were removed with the rock substrate still attached to the base, the majority separated cleanly from the substrate.

CLATHROMORPHUM COMPACTUM (NORTH ATLANTIC, LABRADOR SEA, AND ARCTIC)

More than 200 stations, at depths ranging from approximately 0 to 35 m, including the Gulf of Maine, Nova Scotia,

the Gulf of St. Lawrence, the island of Newfoundland, and the Labrador coast northward to Cape Chidley, were sampled by Walter Adey and his students. The Gulf of Maine (GOM) specimens were collected primarily from 1960 to 1963. Some of the Labrador (LAB), northeast Newfoundland (NENF) and northern Gulf of St. Lawrence (NGSL) specimens were collected during a 1964 cruise, and a limited number of photographic bottom images are available from that cruise. However, the majority of the *C. compactum* specimens were collected during expeditions of the R/V *Alca i* during the summers of 2010 and 2011. The research base comprises

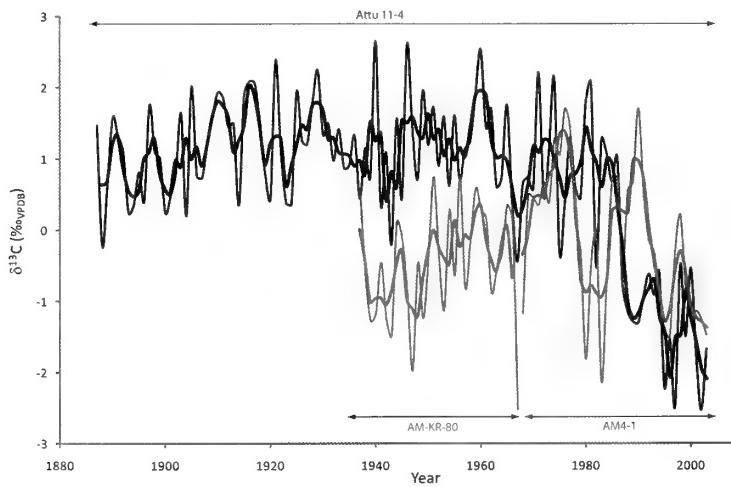


FIGURE 6. Annually resolved $\delta^{13}\text{C}$ values for three *C. nereostratum* specimens collected off two Aleutian Islands with the 3-year running mean in bold. (Williams et al., 2011).

approximately 4,000 specimens of coralline algae, including *C. compactum*, now housed at the Smithsonian's National Museum of Natural History in Washington, DC. These collections have not been formally accessioned to the U.S. National Herbarium, but are available by contacting the first author. During the 2010–2011 cruises, the bottoms from which the collections were taken were extensively documented with digital still images and video. This digital image archive will be available with the collections. A single large sample of several fused plants, partially reported here, was collected by M. Goobie and E. Edinger at Arctic Bay in northern Baffin Island at 72°N. Digital images of the cor-strome bottom in Arctic Bay are available with the collection.

CLATHROMORPHUM NEROSTRATUM (ALEUTIAN ISLANDS)

Three important *C. nereostratum* specimens utilized in this study were collected by Lebednik (1976) at Amchitka; two others were collected by R. Steneck in 2004. The remainder of the material (21 specimens) was collected in the summer of 2008 by Jochen Halfar (JH, with S. Hetzinger and R. Steneck) on a cruise from Akun Island (165°W) in the east to Attu Island (175°E) in the western Aleutian chain.

SPECIMEN PREPARATION

Many of the specimens collected from 1960 to 1964 were diamond sawed into smaller blocks and then fixed, decalcified, and microtome sectioned in paraffin before being studied with a compound light microscope. A large microscope slide collection remains part of this material. Recently collected large specimens were usually first cut with a diamond saw and then fractured (essentially randomly) with wire cutters. Fragments with the desired orientation were then selected for mounting and then carbon coated for examination with a Leica Stereoscan 440 scanning electron microscope (SEM).

Hiatella arctica is an abundant mollusk clathrostrome borer, especially in the Labrador Sea but also in the Aleutian Islands (Chenelot et al., 2011). Shells of this bivalve are relatively soft and ill suited to scraping; burrows are clearly constantly enlarged by dissolution of the *Clathromorphum* skeleton, perhaps by release of an acid. The net effect this enlargement is a natural etching of the coralline skeleton. Burrow walls were extracted by diamond sawing followed by wire cutter trimming. The appropriate surfaces, carbon coated for SEM examination, have been invaluable for understanding biological and mineralogical patterns.

The SEM images were typically taken at 50 \times , 500 \times , and 3,000 \times (occasionally at 10,000 \times) as appropriate to the data sought. Although many single images were utilized, especially of cellular and calcification features, often multiple images were compiled into mosaics of vertical fractures. These mosaics allow large-scale examination of conceptacle and anatomical layering as well as the determination of the vertical growth pattern over time. Conceptacle-based growth rates were determined by

Hiatella cavities. Conceptacle dimensions were obtained by measuring all conceptacles in a mosaic for which the pore plate could be clearly discerned. Seasonal stages of reproduction were estimated by examining multiple, haphazardly selected specimens with a dissecting microscope.

TERMINOLOGY

In this volume we use modified classical terms for coralline anatomy. Hypothallium applies to the basal cell filaments, where the long axis of the cell is parallel to the substratum (in *Clathromorphum*, multiple layers of cells grow parallel to the substratum). The bulk of the thallus, built with filaments whose cells have their long axis perpendicular to the substratum, is termed the perithallium. When the intercalary meristem was first described (Adey, 1964), two new cell types, the meristem itself and the photosynthetic epithallium (previously called cover cells) distal to the meristem, were added to the lexicon. In *Clathromorphum*, the cells of both perithallial and hypothallial filaments become linked horizontally by fusion tubes that serve to transport metabolites. Epithallium, perithallium, and hypothallium are primary tissues; additional secondary tissues are formed in reproduction and wound healing as we shall describe in this volume.

RESULTS

REPRODUCTION

Like most corallines, *Clathromorphum* species have a basic red algal triphasic life cycle in which isomorphic 2n (diploid) plants (asexual in much of the literature) bear either n (haploid through meiosis) or 2n spores in sporangia, which are in turn borne in reproductive structures called conceptacles. The 2n spores produce new (asexual) spore-bearing plants. The n spores, on the other hand, produce separate isomorphic male and female plants. Both male and female plants produce either spermatangia or carpogonia (egg cells) in similar conceptacles that are typically considerably smaller than the asexual conceptacles. When the carpogonia are fertilized by the amoeboid spermatia released from the spermatangia, they produce fusion cells that in turn develop filaments bearing 2n carpospores. This set of 2n filaments, borne on the n female plants, is sometimes referred to as a carposporophyte generation. The carpospores give rise to the 2n (asexual) generation (Adey, 1965; Lebednik, 1976). The maturing sporangia and/or their spores of both asexual and carposporophyte conceptacles dissolve the calcified perithallium surrounding the conceptacle, considerably enlarging the

conceptacle. Whereas sexual and cystocarpic gametangial conceptacles have a single large pore at their apex, asexual sporangial conceptacles are multiported.

Sporangial (apparently diploid) plants (with abundant bi- or tetrasporangium-bearing conceptacles) are seasonally common among the principal *Clathromorphum* species, whereas gametangial plants (apparently haploid male and female) and conceptacles are more or less rare. Adey (1965) examined reproduction in *C. compactum*, and Lebednik (1976) extensively studied reproduction in *C. nereostratum*. Herein we provide additional information for both species. The earlier work by Adey and Lebednik was accomplished with decalcified material studied with light microscopes. Here we emphasize SEM sections, observing the conceptacles as they occur buried in the fully calcified skeleton. The diameter and height of sporangial conceptacles for both species and for sexual conceptacles of *C. nereostratum* are given in Figure 7. Complete dimensional analyses of surficial,

mature conceptacles, with roof dimensions and burial depth at maturity, are provided in Adey (1965) and Lebednik (1976). Since gametangial conceptacles develop in spring rather than autumn (when sporangial conceptacles develop), distinguishing between them may be necessary in temporal analyses of tissue chemical composition.

Adey (1965; for *C. compactum*) and Lebednik (1976; for *C. nereostratum*) provided photographic images of several stages of development of sporangial conceptacles. However, neither author showed the details of development, particularly relative to the simultaneous and essential growth in vegetative tissue, that are required for understanding the relationship between anatomy and seasonality. This information is potentially important in climate archiving for determining the seasonality of carbonate deposition in each vegetative cell. Figure 8 shows the stages of development of sporangial conceptacles in *C. compactum* relative to the surrounding vegetative tissue. Developmental stages

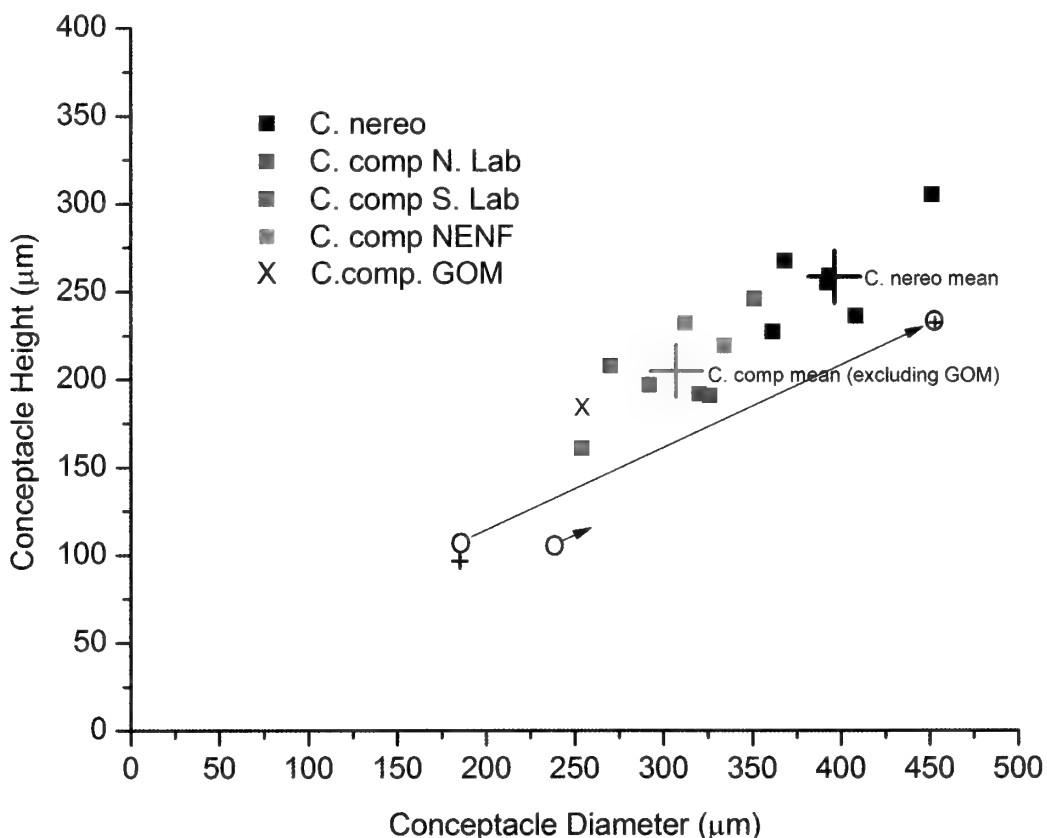


FIGURE 7. Dimensions of mature conceptacles of *C. compactum* (105 conceptacles, 13 plants, and 9 stations) and *C. nereostratum* (84 conceptacles, 11 plants, and 7 stations). Colored squares are means of individual plants. Female conceptacle data are for *C. nereostratum* Lebednik, 1976. Male and cystocarpic data are derived from a combination of this study and Lebednik (1976). The long arrow describes the path of development of *C. nereostratum* female conceptacles, from unfertilized carpogonia through postfertilization to mature carposporangia.

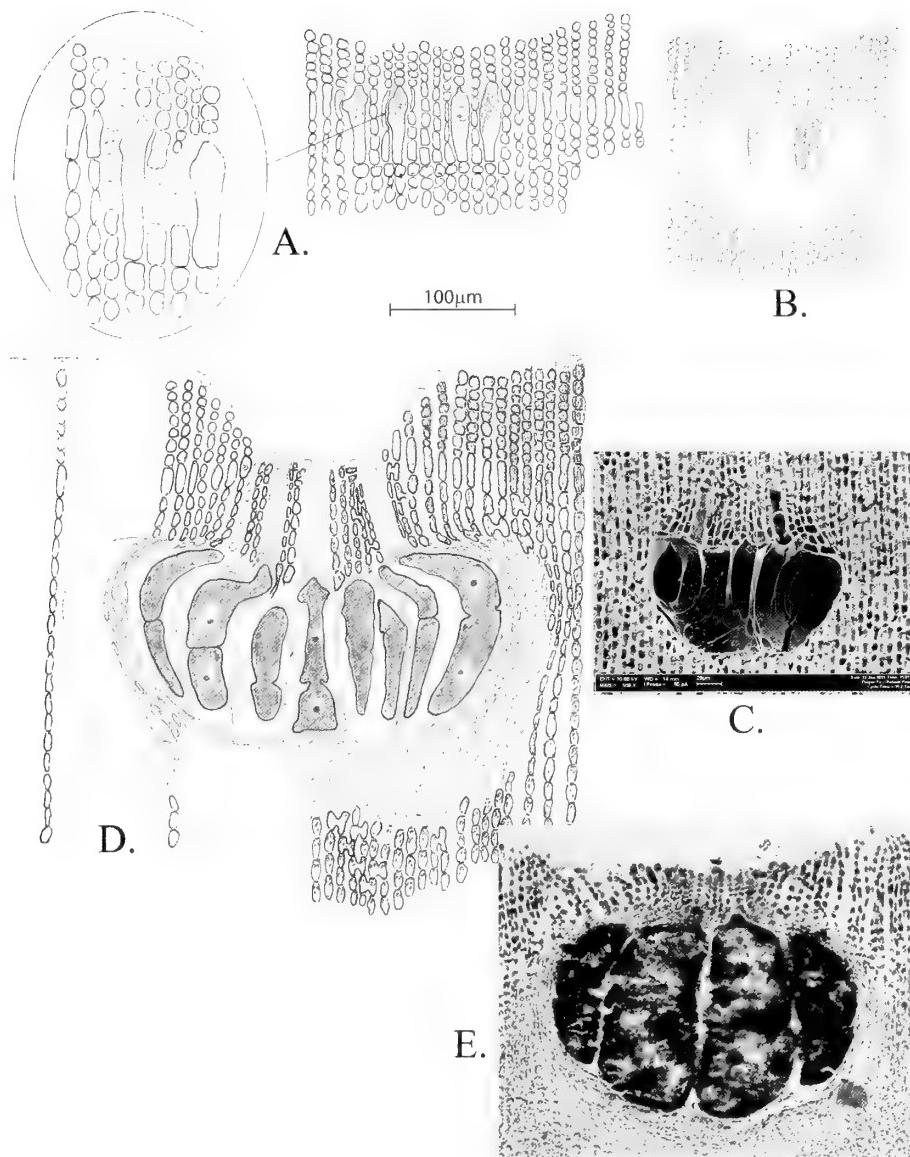


FIGURE 8. Development of asexual, bispore-producing *C. compactum* conceptacles described from specimens collected in the northeastern Gulf of Maine. (A) Early sporangial mother cells and distinctive supporting cells (September–October). Fertile disk (nemathecium) 100–120 μm in diameter; it expands vertically, without primary calcification (sporangia or intersporangial filaments), to form a fertile uncalcified cylinder. Initiated as meristem cells at 10–20 μm of length, sporangia expand vertically, accommodated by growth in the surrounding calcified vegetative tissue. (B) Later stage: sporangia over 100 μm in length with a thick, organic, apical wall or cuticle (to form spore release pore). Here a decalcification “front” below and to the sides of the fertile cylinder is seen; cell crushing has yet to occur. Eight to 12 vegetative cells have developed in the surrounding vegetative crust to allow sporangial growth. (C) SEM image of an aborted conceptacle just prior to the stage shown in B (northern Labrador). (D) Later stage with further decalcification; sporangial enlargement laterally and some crushing of surrounding vegetative cells. The overlying epithallial cells have broken off to expose the conceptacle roof (white disks seen from surface). A later surface view of this stage is shown in Figure 9C, D. (E) Light microscopic image of mature conceptacle at full, mature dimensions (December–January), with decalcification and crushing of lateral and underlying vegetative cells, and spores forming inside the sporangia. A, B, and D were drawn from microtome sections of winter plants. C is a SEM image of a calcified, fractured section. E is a decalcified and stained microtome section. All images are at the same scale, indicated by the bar.

of *C. nereostratum* are not shown in similar detail since full seasonal, decalcified, and sectioned material is not available. However, it is clear from preliminary analyses that the patterns are very much the same.

Reproduction in *Clathromorphum compactum*

Adey (1965) demonstrated the seasonally determined development of sporangial conceptacles in *C. compactum* in the Gulf of Maine, where conceptacles are initiated in early autumn (September and October), reach maturity in midwinter, and are

fully overgrown by late spring. The farther north *C. compactum* plants grow, the later their reproductive maturity is; in northern Labrador, most plants are at the peak of the reproductive cycle in midsummer, the surficial conceptacles being full of ripe sporangia (Figure 9; Table 1). Conceptacle initiation is likely controlled by the photoperiod, with light rapidly diminishing in September and October; temperature is likely not a significant factor as there is a considerable difference in temperature from south (approximately 10°C) to north (approximately 5°C) at this time.

The developmental morphology of a typical sporangial conceptacle of *C. compactum* from southern Labrador is shown in

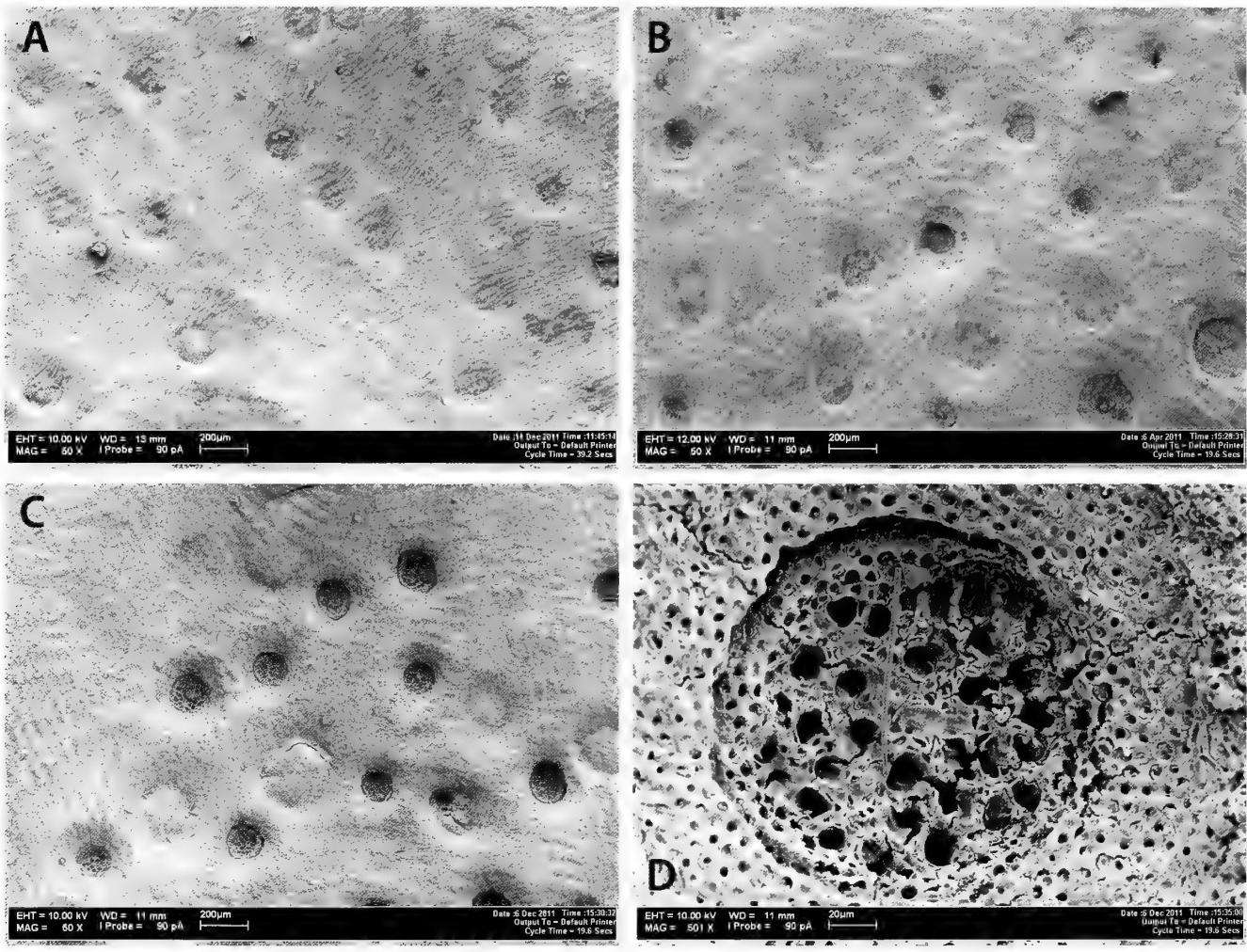


FIGURE 9. SEM images of typical *C. compactum* surfaces from different regions showing reproductive state during midsummer (see Table 1). (A) Northeastern Newfoundland, conceptacles mostly grown in, but remain clearly visible. (B) Southern Labrador, conceptacles ranging from immediately postmature to grown in. (C) Northern Labrador, conceptacles mostly fully mature; the low mound in the lower center is a submature conceptacle with a conceptacle cap not fully broken out. (D) Conceptacle roof at larger scale; pores for exit of the spores are mostly free of sporangial cap walls; a few dried pore plugs remain. During summer in the Gulf of Maine, conceptacle roofs with visible pores are not found, and only faint conceptacle “ghosts” appear in 60%–70% of the population. Note the strong chiton grazing marks in A and C and also in B, although somewhat grown out.

TABLE 1. Summer reproductive state as a percentage of specimen surface.

Subregion	Not reproductive ^a (%)	Initial state ^b (%)	Mature conceptacles (%)	Conceptacles growing out (%)	Faint conceptacle remains (%)
Northern Labrador	19	0.3	40	36	3.5
Southern Labrador	32	0	32	31	4.5
NE Newfoundland	62	0	3	15	20
Northern Gulf of St. Lawrence	52	0	Trace	3.1	45
Gulf of Maine ^c	30	0	0	10	60

^aMidsummer (July–August) reproductive (asexual) state in *Clathromorphum compactum* from northern Labrador to the Gulf of Maine. The values for each of the Subarctic subregions are estimated from 40 haphazardly selected sets of undamaged specimens with a 20–50 cm² surface, estimated using a dissecting microscope.

^bConceptacle caps.

^cFrom Adey (1965).

Figure 10A. The sporangial caps (plugs), which are embedded in the calcified conceptacle roof tissue, and the uncalcified sporangial mother cells are together about 150 µm long at maturity (before spore formation). The sporangia and surrounding vegetative filaments form a developmentally uncalcified fertile cylinder that is approximately 100 µm in diameter and 100 µm long before final expansion to sporangial maturity. As we shall show, fertile cylinder development requires the accompanying production of about 10–12 cells in each filament of the surrounding vegetative tissue. Near sporangial maturity, the carbonate component of an 80-µm-thick underlying vegetative tissue is dissolved beneath the enlarging sporangia, with an additional 70–80 µm of carbonate also dissolved laterally, to make room for the large sporangia to fully mature. The sporangia produce bispores, each of which is approximately 1,000 times greater in volume than the individual surrounding vegetative cells. The total noncalcified, organic volume of crushed vegetative cells is approximately equal to the final spore volume. In the southwestern Labrador Sea, this final expansion phase occurs in late spring and early summer, just after ice breakup, when available light should be at a maximum. Figure 10B, reduced to show primarily sporangial development, provides a mean pattern for northern Labrador, where conceptacle maturation is delayed even longer into the next summer.

Sporangial conceptacle development is initiated in early autumn, and at maturity carbonate solution and crushing of previously formed summer vegetative tissue occurs to about 80 µm below the plane of sporangial initiation. In southern Labrador and northernmost Newfoundland, there is a greater level of vegetative cell fusion for a limited period at the time of sporangial initiation. This cell fusion creates a weak zone in the carbonate, and horizontal fractures are easily induced on this plane, as can be seen in Figure 11.

As shown by Adey (1965) for the Gulf of Maine and here for the core Subarctic (Table 1), 20%–30% of the plant surface in each year does not become reproductive. This is seen in an

analysis of conceptacle bands in a *C. compactum* plant from Labrador (Figure 12A,B), where every fifth to seventh year a growth ring is devoid of a conceptacle band. Specimens have been found in which extensive conceptacle production has occurred for several consecutive years, followed by years with few or no conceptacles (Figure 2B). In one very old specimen from northern Labrador, several hundred years' worth of missing conceptacle bands were seen. This phenomenon implies that anatomy must be consulted, in addition to measuring the number of conceptacle bands or the thickness between bands, in order to obtain an accurate yearly archive. If it is suspected that several years are missing, this suspicion is relatively easy to confirm with anatomy. If conceptacles were apparently missing for many years, it would be necessary to confirm by counting each year's Mg cycle. As shown in Figure 12B, broken-out conceptacles can "grow in" by regrowth of vegetative cells from the base and sides, nearly obliterating evidence of the presence of the conceptacle in a superficial analysis. The perithallial tissue that has grown back into the conceptacle cavity will have formed several months later than the surrounding tissue, depending on geographic latitude.

In the specimen shown in Figure 12B, the years 2005 and 2006 lack buried conceptacles. For the year 2007, a broken-out conceptacle appears on the right (note the presence of a full conceptacle farther to the left). During the summer following breakout, new tissue formed at the base of the conceptacle and refilled the cavity during the following summer. This new tissue was formed months later than the surrounding vegetative tissue. A laser scan passing through the broken-out and grown-in conceptacle would show carbonate chemistry totally out of phase with that of the larger specimen on the same plane, unless the presence of this grown-out conceptacle were taken into consideration. Conceptacle cavities are oblate spheroids; because sporangial formation begins in autumn (see Figure 10), a horizontal plane through the principal diameter of the spheroid approximately marks the beginning of October.

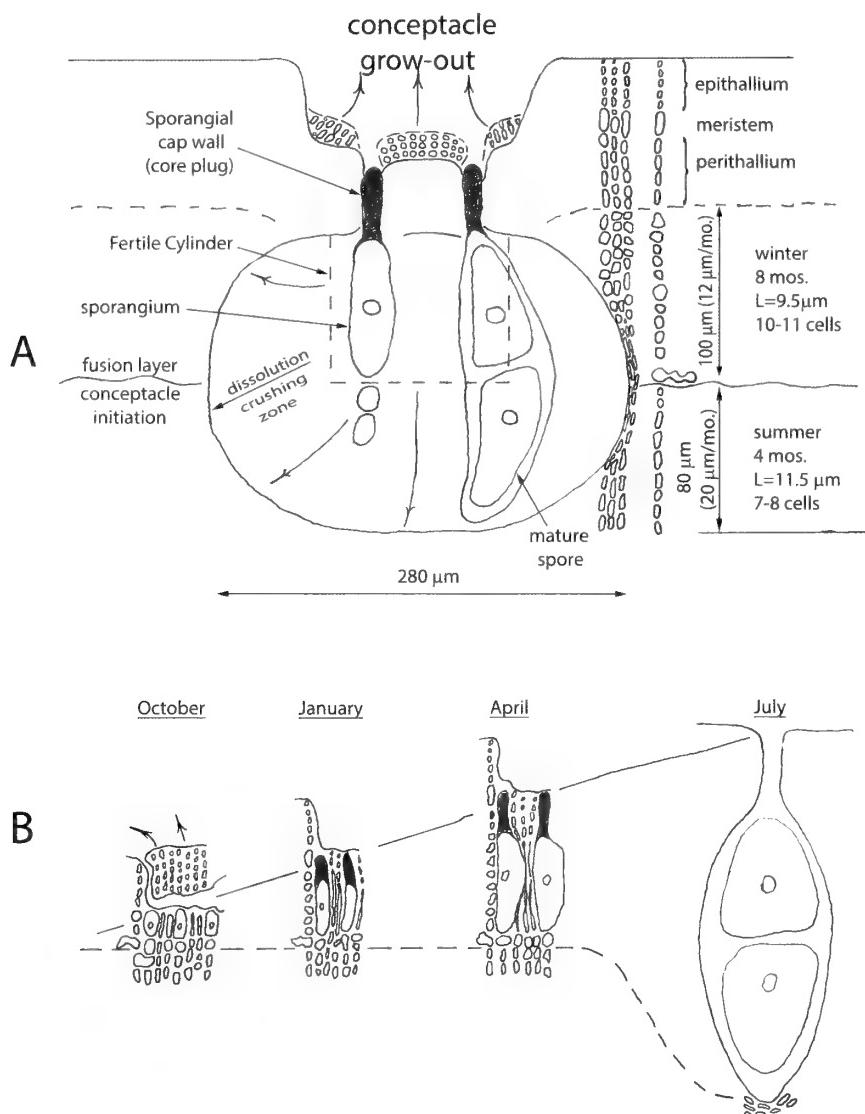


FIGURE 10. *Clathromorphum compactum* conceptacle and sporangial formation. (A) Dimensional and cellular development of average bisporic conceptacle in southern Labrador relative to season and vegetative tissue. Numbers to the right are averages and can vary with region of development. (B) Sporangial development with time in northern Labrador. In the Gulf of Maine, because of higher vegetative growth rates, this process occurs from October to January.

Reproduction in *Clathromorphum nereostratum*

A detailed developmental analysis of reproduction in *C. nereostratum* is not available and would require a set of specimens taken in the Aleutian Islands throughout the autumn. Nevertheless, the photographic images published by Lebednik (1976) are adequate to show that the pattern is similar enough to that of *C. compactum* to allow the use of Figure 8 (developed for Gulf of Maine populations) but not Figure 10 (developed

for Labrador). However, there are a number of additional differences that are critical to interpretation for climate archiving.

Of the 26 specimens of *C. nereostratum* examined from the Aleutian Islands, 24 were collected in summer (June–August) and 2 in December. Of the 24 specimens collected during the summer, 2 had single-pored gametangial conceptacles at their surface. One of these two plants had mature fertilized female conceptacles (carposporangial conceptacles), whereas the other had postprime male conceptacles with open pores remaining.

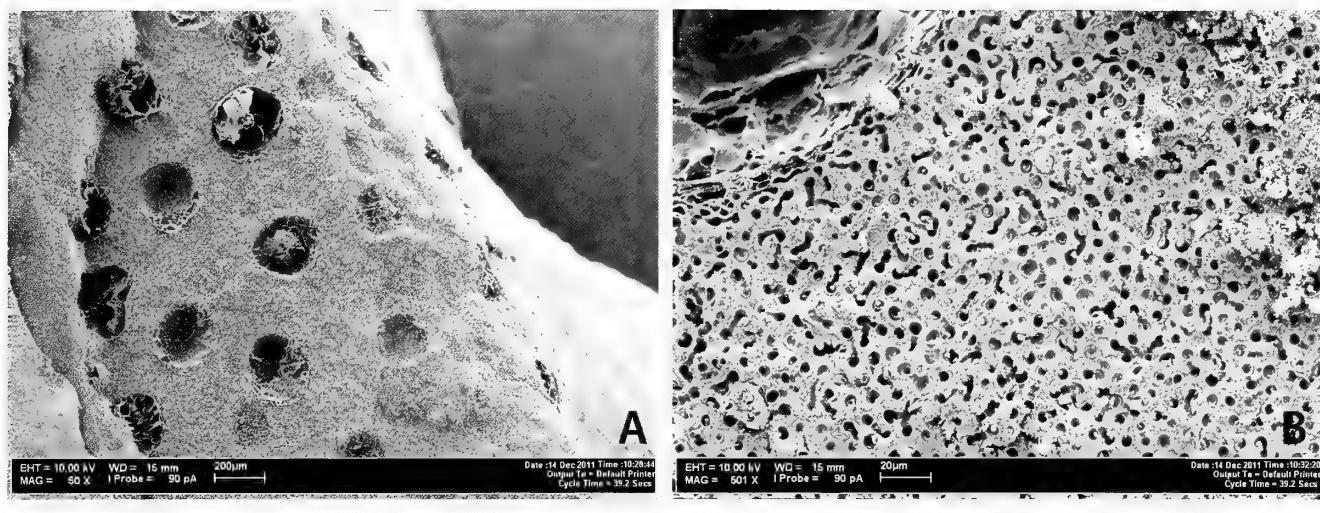


FIGURE 11. Horizontal fracture in a specimen of *C. compactum* collected in summer of 2010 (Great Northern Peninsula of Newfoundland). (A) The narrow bench to the left is the meristem fracture zone. (B) The main fracture bench (center in A) occurred on a plane with a high level of cell fusion in the autumn of 2009 (when sporangial development initiated). Also visible is the transition from summer to winter in perithallial tissues.

Although degenerate (broken-out) or faint ghosts of growing-in sporangial conceptacles were sometimes present in the remaining 22 specimens and buried sporangial conceptacles were present in section, no mature, multipored sporangial conceptacles were seen at their surfaces. In section, the most recent band of buried conceptacles occurred about 100 µm below the meristem, indicating maturity the previous winter.

Both specimens collected in December presented premature to mature sporangial conceptacles (Figure 13A). It is not usually possible in SEM images to distinguish between bisporangia and tetrasporangia in buried conceptacles (the latter likely indicating meiosis and reduction to the haploid state in the spores). However, both December specimens presented tetrasporangia, and Lebednik (1973) found only tetrasporangial conceptacles in this species. Although the data are minimal, this finding suggests that *C. nereostratum* generally has the triphasic and isomorphic alternation of generations described earlier. In this case, sporangial (2n) plants reproduce in autumn, maturing in winter (as in *C. compactum* in the Gulf of Maine and Nova Scotia) and gametangial (1n) plants reproduce in spring, maturing in summer.

On the basis of available collections, gametangial plants are probably infrequent in *C. nereostratum* (very extensive collections demonstrate rarity in *C. compactum*). Thus, especially in *C. nereostratum*, it is essential to identify the type of conceptacle (sporangial or gametangial) in order to determine the developmental timing of the conceptacle compared to the vegetative tissue. Male and female conceptacles are quite small compared to sporangial conceptacles; although both become buried, they are not likely to be confused for sporangial conceptacles (Figures 7, 13). Fertilized female conceptacles (producing carposporangia)

are somewhat larger in diameter than sporangial conceptacles (Figures 7, 13). However, they are not as tall, suggesting that carposporangial tissue dissolution is not as extensive beneath the conceptacle. Since carposporangia are produced only laterally from fertilized carpogonia (egg cells), centrally there is no dissolution, resulting in the formation of a central columnella, leading to dumbbell-shaped conceptacles. For a detailed description of the development of sexual conceptacles in *C. nereostratum*, see Lebednik (1976). Carposporangial conceptacle development has not been described in *C. compactum*, but it is likely quite similar. The presence of a central columnella and dumbbell-shaped conceptacles shows that it is the developing sporangia (bisporic, tetrasporic, or carposporic), not the vegetative cells, that provide the acid for surrounding carbonate dissolution.

Female conceptacles are located midway through the yearly cycle (Figure 13B,C), with a sharp perithallial boundary in late autumn (see below). On the other hand, sporangial conceptacles are located near the upper (later) boundary of the cycle (Figure 13A). In medial sections, sporangial conceptacles are oval in shape, whereas female conceptacles are dumbbell shaped, with a central columnella. In sporangial conceptacles, the recalcified sporangial walls are vertical, whereas the female conceptacle carposporangia and supporting structures appear as packed spheres of many sizes (Figure 13B).

CELLULAR AND ANATOMICAL STRUCTURE

Aside from a basic pattern of upright filaments of cells combining to form a calcified mat showing vague "rings," the perithallial vegetative anatomy of *Clathromorphum*, as seen in

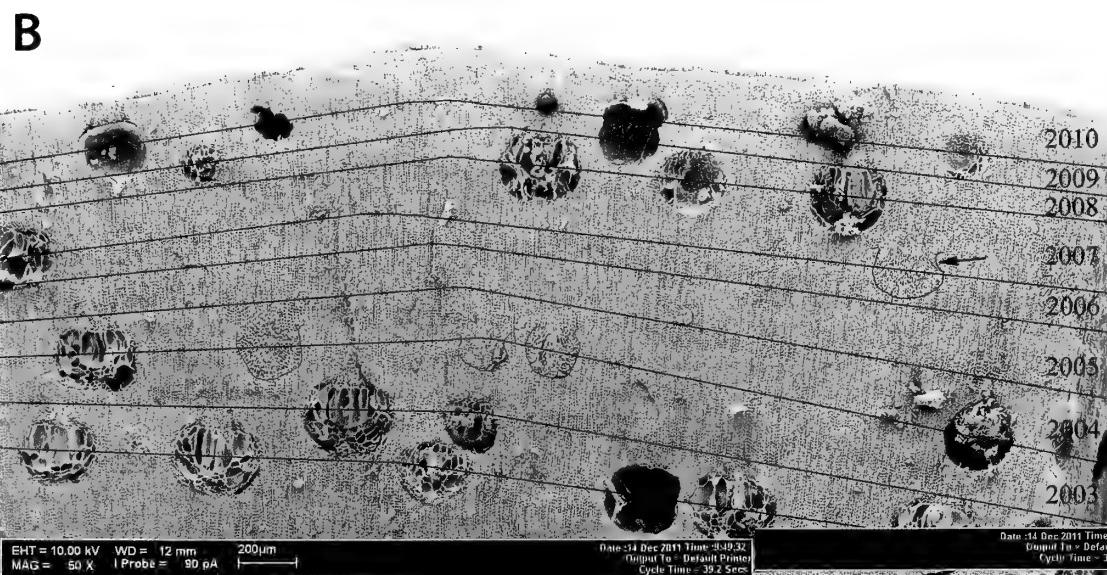
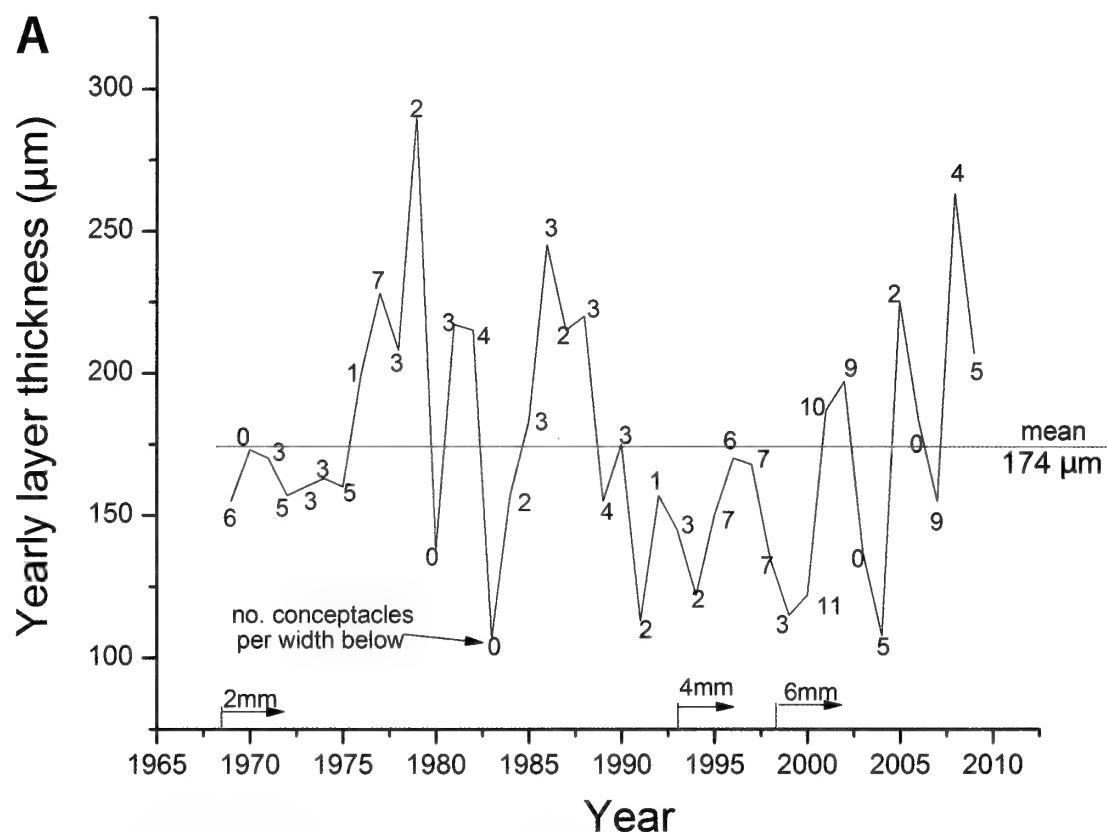


FIGURE 12. (A) Thickness of yearly bands in *C. compactum* from southern Labrador (specimen 10-7S (1a)). The number of asexual conceptacles in each band, in the limits of the SEM mosaic, is indicated. (B) SEM of *C. compactum* from the Great Northern Peninsula of Newfoundland, showing yearly bands of conceptacles. This is a faceted specimen, with the facet boundary represented by the abrupt change in the slope of the conceptacle planes and ragged vertical lines on the left (see Figure 18). A broken-out conceptacle (2006/2007) is shown by the arrow on the right, with tissue formed from the base of the conceptacle refilling cavity; this tissue formed months later than the surrounding vegetative tissue.

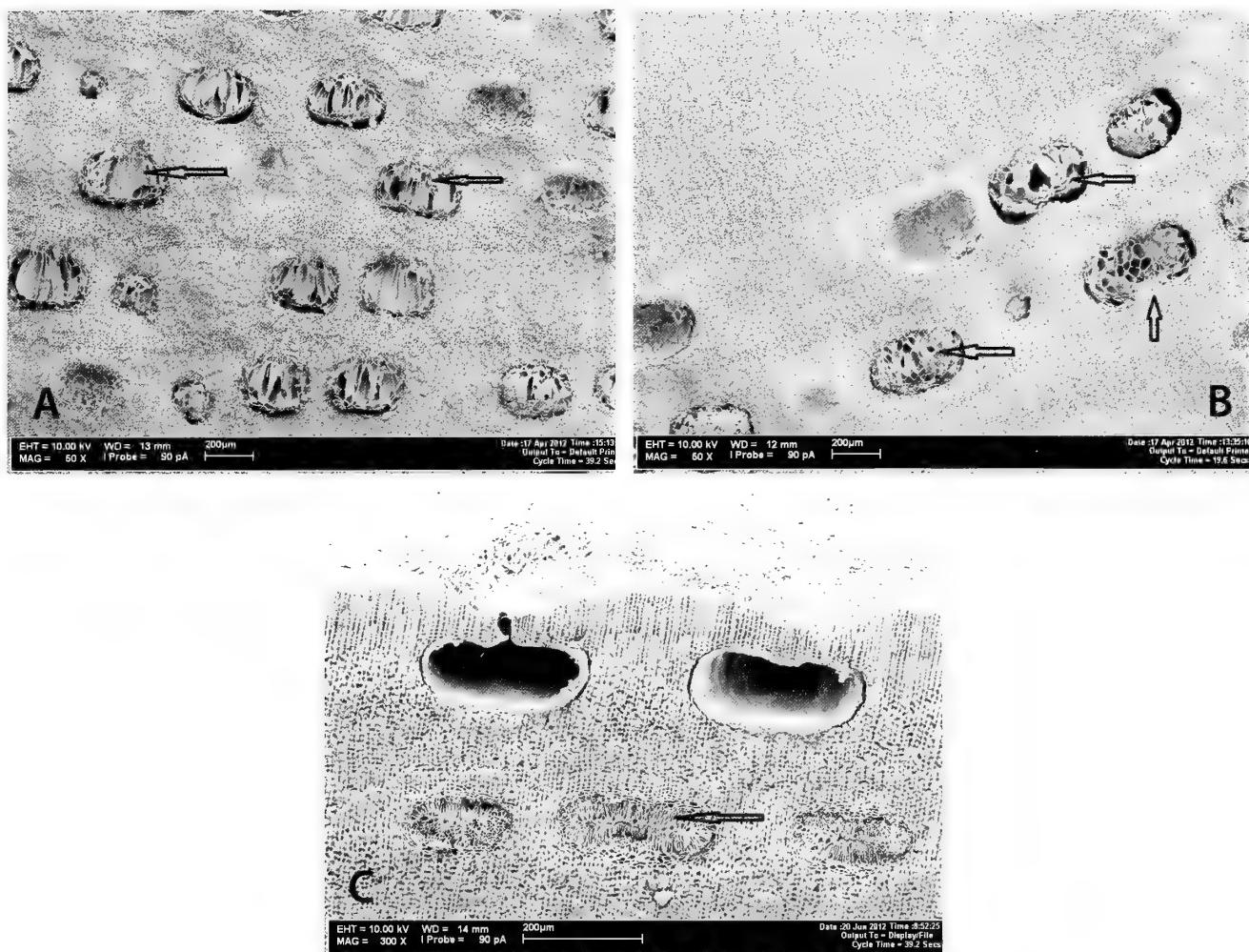


FIGURE 13. *Clathromorphum nereostratum* conceptacles in SEM images. Note that recalcified sporangium cell walls tend to be vertical in asexual conceptacles (A; reflecting vertical orientation of sporangia), whereas cystocarpic conceptacles (B) appear as small angular circles of various sizes (left arrow in B; cells of gonimoblast filaments [upper arrow] produce cystocarpic sporangia laterally). (A) Yearly layers of buried bi- or tetrasporangial conceptacles (sporangial walls recalcified after burial; arrows). (B) Mature female (cystocarpic) conceptacles. Midsections show a dumbbell shape (bottom right arrow) because of dissolution of the surrounding carbonate by peripherally developed spores. (C) Small, ovoid, male conceptacles with recalcified spermatangial mother cell walls (arrow).

a dissecting microscope view of a vertical fracture or polished slice, may superficially appear to be without structure. However, at higher magnification, it is seen to be a rich mosaic, deriving from the genetic control of cellular and tissue development as influenced by the physical and biological environment. Measurements of cell dimensions in SEM images demonstrate this genetic-physical interaction. As shown in Figures 14A, 14B, and 15, cell dimensions change seasonally. Cells within each filament are linked by pore plates (pit connections and pit plugs in most red algae), and the length, pore plate to pore plate, varies more or less consistently from about 8 to 15 μm for both species; the cell lumen diameter likewise ranges from 2 to 6 μm . There is a strong tendency for cells to be shorter and wider in the winter and early spring, with a lengthening and narrowing of the lumen

in the summer and early fall (Figures 14A, 14B, 15). This pattern is strongly apparent in most *C. nereostratum* specimens from the Aleutian Islands but less so in *C. compactum* specimens from the northwestern North Atlantic.

Since total filament diameter, including the calcified cell walls, is fixed at roughly 10–11 μm in *C. nereostratum* and 9–10 μm in *C. compactum* (except when filament branching and tissue expansion is occurring), it is the total calcified cell wall thickness that changes seasonally (Figure 16A,B). As can be seen clearly in Figures 16 and 17, there is a well-defined inner wall, with small, prismatic, radially oriented calcite crystals that maintain about the same length (1 μm) and character throughout their distribution and annual cycle. This wall type has been described for most corallines for the last several decades

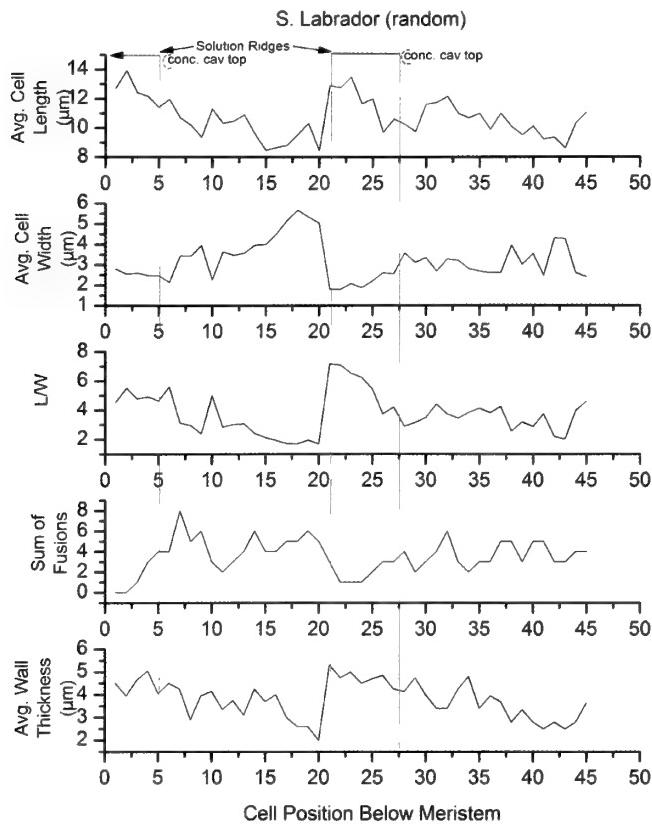


FIGURE 14A. *Clathromorphum compactum* variation in cell dimensions with depth in perithallium: mean perithallial cell dimensions, as measured in two crusts, from meristem, with depth (summer collected in southern Labrador; mean of two consecutive years, three cell rows). L/W = length/width.

(reviewed by Adey, 1998; see also Adey et al., 2005). However, in *Clathromorphum* species, especially during summer and autumn, the space between the filaments becomes filled with much larger, often spear-shaped, vertically or diagonally oriented calcite crystals (interfilament crystals). As shown in Figure 17C, the inner-wall crystals are formed within the organic membranes of the cell, whereas the deltoid interfilament crystals are formed in the cavity between the filaments (Figures 16A, 17B,C). This phenomenon is coincident with the narrowing of cell lumens. Interfilament crystals tend to be present year-round. However, in winter they are far less abundant, the cell lumens being larger in diameter. Thus, summer and fall tissue is considerably denser than winter tissue.

Unlike the closely related, sheet-forming species *Clathromorphum circumscripum* (which occurs in shallower water and tide pools), mature *C. compactum* tends to be dome shaped. Large sheetlike (clathrostrome) formations often develop, especially in the northern Subarctic, but they form from the coalescing of adjacent *C. compactum* plants. Although smooth, dome-shaped,

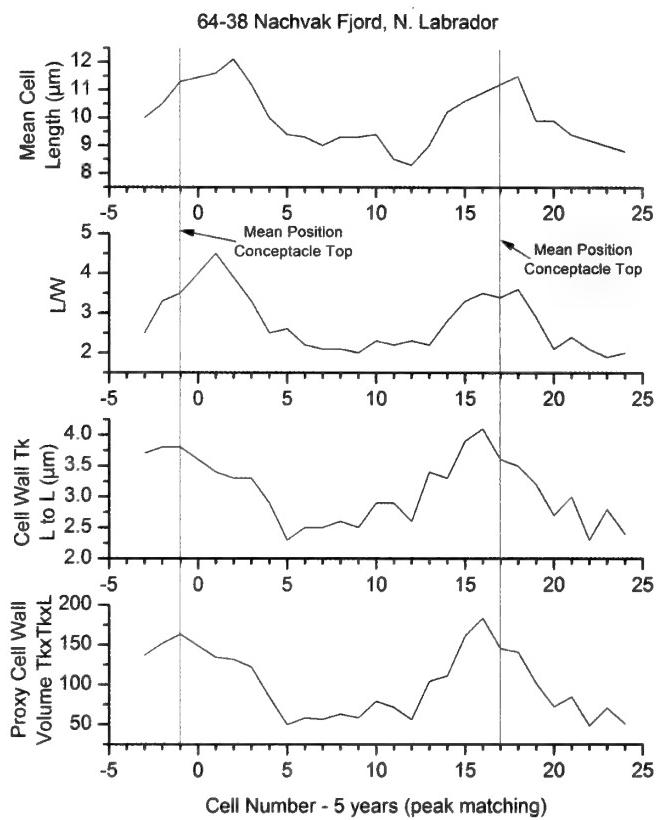


FIGURE 14B. *Clathromorphum compactum* variation in cell dimensions with depth in perithallium: mean dimensions from five continuous years, matched peak to peak (summer collected from northern Labrador). L/W = length/width; Tk = thickness

individual plants are common, especially in the warmer part of the *C. compactum* range, domes featuring more or less flat facets separated by slightly grooved ridges are more typical (Figure 18). Facets arise when the scattered filament branching required to form the domed morphology of *C. compactum* occurs in localized vertical planes. Facets can shift with time or split in two for several years. Conceptacles generally do not form near facet boundaries; when a facet does develop, previous nearby conceptacle areas can become nonreproductive. Also, different facets on the same plant can grow at different rates. For that reason, growth rates in mound-forming *C. compactum* are taken in the middle of the dome.

Clathromorphum nereostratum can develop into a much thicker crust (up to 50 cm) than *C. compactum* (up to 12 cm). This is partly due to the much slower growth of *C. compactum* in the colder water of the core Subarctic and Arctic (see below). The crust thickness achieved by *C. compactum* in warmer Labrador waters, for example, is comparable to that of *C. nereostratum*, taking into account the difference in the yearly growth

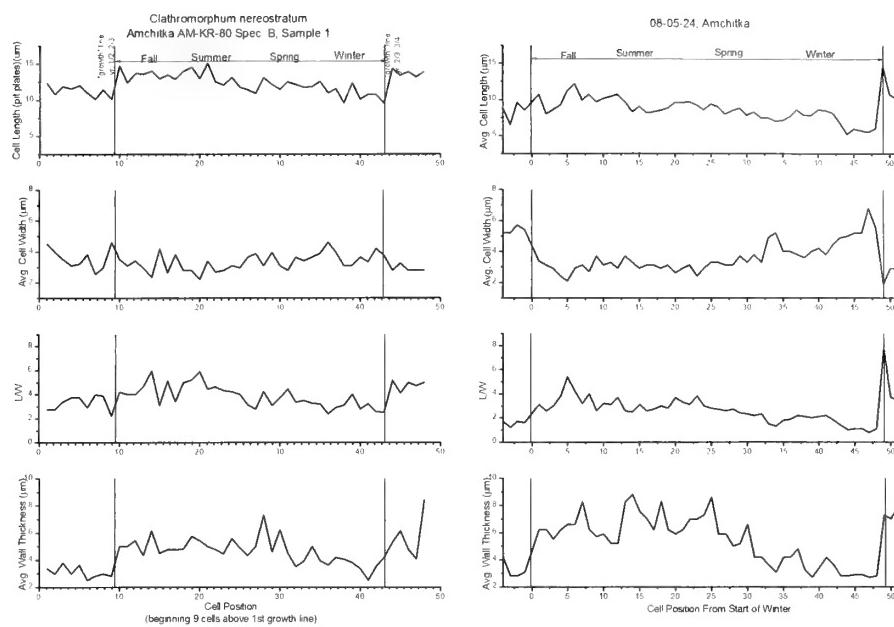


FIGURE 15. *Clathromorphum nereostratum* cellular anatomy. Cell dimensions with depth in perithallial tissue. (left) Amchitka plant taken in the 1970s. Mean cell dimensions, two successive years. (right) Plant from Amchitka, taken in 2008. Mean, three parallel filaments, single year.

rates. However, even in the Gulf of Maine, the southern limit of *C. compactum*, where the yearly mean temperature and growth rates are similar to those of *C. nereostratum*, *C. compactum* plants remain much thinner. This is partly due to the “leafy” growth morphology of the hypothallium (the basal tissue that grows parallel to the substrate) of *C. nereostratum*. In *C. compactum*, the hypothallium has a mean thickness of 3.5 cells (maximum 6 cells) and 22 μm (maximum 43 μm), and the cells are tightly adherent to the substrate (Adey, 1965). In *C. nereostratum*, on the other hand, the hypothallium has a mean thickness of 16.8 cells (maximum 24) and 135 μm (maximum 206 μm; Lebednik, 1976); the growing margin is thick enough to be structurally freestanding and often becomes cantilevered off the substrate for a considerable distance.

Clathromorphum nereostratum is thus capable of growing over obstacles, and if the growing margin is damaged, a secondary hypothallium, formed from perithallium, grows out over the damaged area (primary hypothallium develops initially from a settled spore on the rock or shell substrate). Individual *C. nereostratum* plants can thus be much broader than those of *C. compactum* (Figure 2F) and have the capability to achieve greater thickness in a single plant. *Clathromorphum compactum* produces a clathrostrome largely by the fusion of many individual small plants. These can be any size, depending upon the recruitment density. At the warmer margin of its temperature limits in the Gulf of Maine, perhaps because of the warmer summer temperatures, which allow greater invertebrate

damage to crusts, and likely because of less successful recruitment, *C. compactum* plants are more scattered and rarely exceed several centimeters in thickness and 100 years of age. As noted above, *C. nereostratum* likely evolved from a *C. compactum*-like ancestor (Adey, unpublished data); the primary innovation was the development of a thicker hypothallium allowing a free-standing cantilevered morphology.

BIOLOGICALLY INDUCED ETCHING AS A SOURCE OF INFORMATION

Hiatella arctica is a common Subarctic bivalve that establishes burrows within the calcified perithallium tissue of *Clathromorphum* crusts. Apparently, *H. arctica* larvae settle at the margin or on a damaged surface of a young plant and are buried by plant growth. The bivalve then grows along with the perithallium, enlarging its burrow by gradually decalcifying the coralline walls surrounding it. If a coralline sample is collected with the animal still alive, the burrow wall can be seen to be etched into ridges and valleys corresponding to the yearly layers of *C. compactum* growth (Figures 19, 20). The etching is probably accomplished with an acid secretion, although localized CO₂ production by the bivalve, accompanied by pH reduction within the confined space of the burrow, could also be a factor. The cell wall carbonate formed in summer, being about two times denser than that in winter, forms the ridges, and the less dense winter cell walls form the valleys. Also, particularly as seen in longitudinal

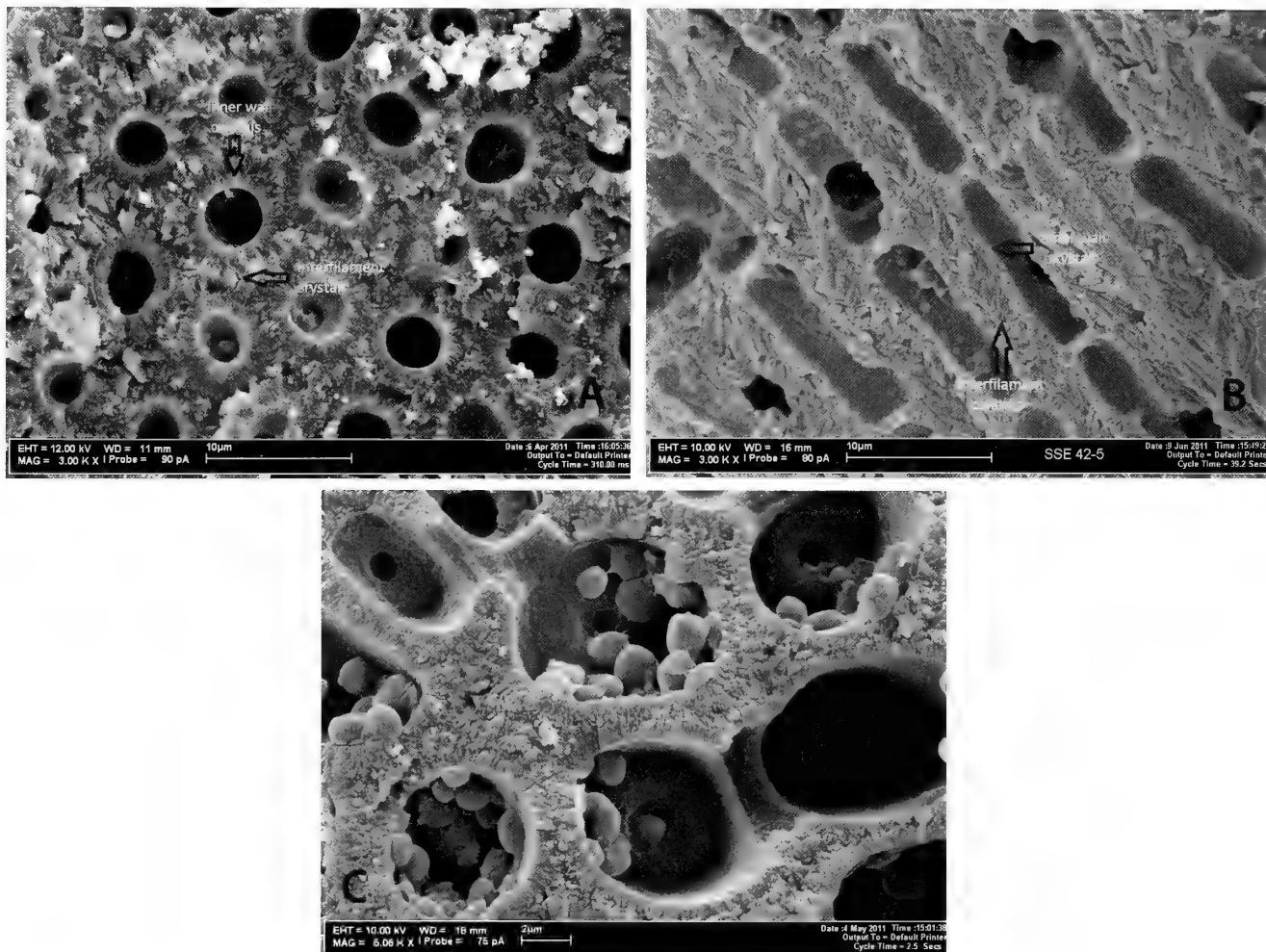


FIGURE 16. *Clathromorphum compactum* calcified wall structure. (A) Transverse fracture showing summer cells with large interfilament calcite crystals between rings of small, radial, inner-wall crystals (crystals 1 μm long). (B) Longitudinal fracture of summer cells showing large, angular interfilament calcite crystals and thin inner walls of fine, radially oriented crystals. (C) Winter cells of fine, radial, inner-wall calcite crystals. Interfilament crystals are only at cell “corners.”

fractures (Figures 16B, 17C,D), interfilament crystals are much larger (to 5–6 μm long) than inner-wall crystals and tend to be arrowhead shaped (Figure 17B).

A closer look at the etched valleys shows that the smaller, radial, inner-wall crystals are more resistant to solution than the larger, vertically oriented, interlamellar crystals. This is a difference in crystal morphology that results in winter cells that tend to break out of the carbonate matrix as silt-sized, hollow grains (Figures 19D, 20A). The inner-wall crystals are embedded in an organic matrix that likely controls their development (Giraud and Cabioch, 1979). Thus, they are somewhat protected from dissolution (Ries, 2011). As discussed below, the interfilament (interlamellar) crystals may be precipitated because of CO_2 removal in the inorganic interfilament space and therefore lack protection from dissolution from an organic matrix.

GROWTH RATE

On the basis of combined analyses of conceptacle bands and cellular anatomy, the thickness of yearly bands in *Clathromorphum compactum* and *C. nereostratum* can be defined using mosaics of SEM images. Further combined with measurements of the bivalve-etched ridges, as described earlier, regional growth rates for *Clathromorphum compactum* are shown in Figure 21. There is a highly significant and consistent drop in overall crustal growth rate from south (Gulf of Maine) to north (northern Labrador and Arctic Bay, Baffin Island). The plants for which these intervals were measured were selected haphazardly from available SEM sections having clearly defined conceptacle bands. No effort has been made to compare the same years in each region, as this would require a more defined ecological depth range for each.

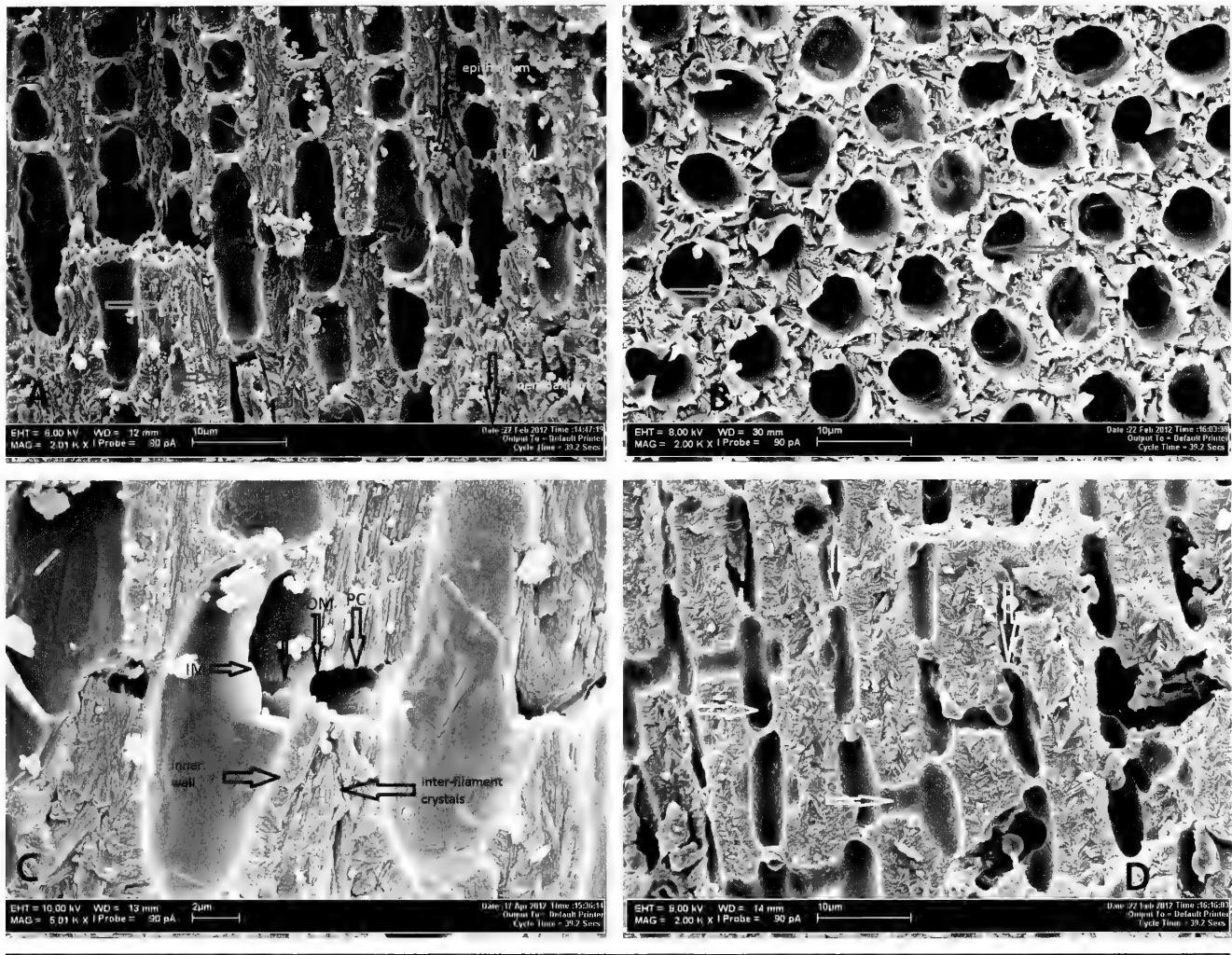


FIGURE 17. *Clathromorphum nereostratum* from the Aleutian island of Amchitka. (A) SEM of vertical fracture with overlying epithallium, underlying perithallium, and meristem with a break in calcification. Inner cell layer of radial crystals (red arrow); vertically oriented interfilament crystals (blue arrow). (B) SEM looking downward into meristem with epithallium removed. A smooth organic material coats the inner wall (red arrow); large deltoid interfilament crystals (blue arrow), apparently with no integral or overlying organic material, lie between the inner wall organic material. (C) Unfractured meristem cells showing the inner-wall inner membrane (IM) and outer membrane (OM), the fractured calcification zone (CZ), and the precipitation cavity (PC). (D) *Clathromorphum nereostratum* from Rat Islands, Aleutian Islands. Summer perithallial cells showing cell fusions formed after burial in the perithallium (horizontal arrows) and pit connections (vertical arrows) between cells of a filament.

The regional growth rates presented in Figure 21 are plotted as a function of yearly mean regional temperature in Figure 22. The Arctic Bay temperature is an estimate based on a 9-month sea ice interval of -1.8°C and a 3-month ice-free interval of 3.5°C . As we will show in a future paper (Halfar and Adey, unpublished), when sea ice is consistently present longer than about 2 months, growth ceases, probably because of a lack of sufficient stored photosynthate. This drop in expected growth relative to temperature is producing a highly significant proxy for sea ice cover. Using the straight-line (GOM to southern Labrador) part of the yearly growth curve with the greatest amount of

information (Figure 22), converted to monthly rates and plotted against the regional temperature curves (Figure 23A), monthly regional growth curves can be derived (Figure 23B). Total yearly growth and the rate of conceptacle maturation (based on the regional height requirement for maturation) can then be summed from the monthly rates. The latter match the data presented in Table 1. Although laboratory-produced growth rates for *Clathromorphum compactum* are not yet available, those for *C. circumscriptum* (Adey, 1970, 1973) suggest that at temperatures below 5°C – 6°C , temperature (and not light) is the primary environmental factor controlling vertical growth. Monthly growth

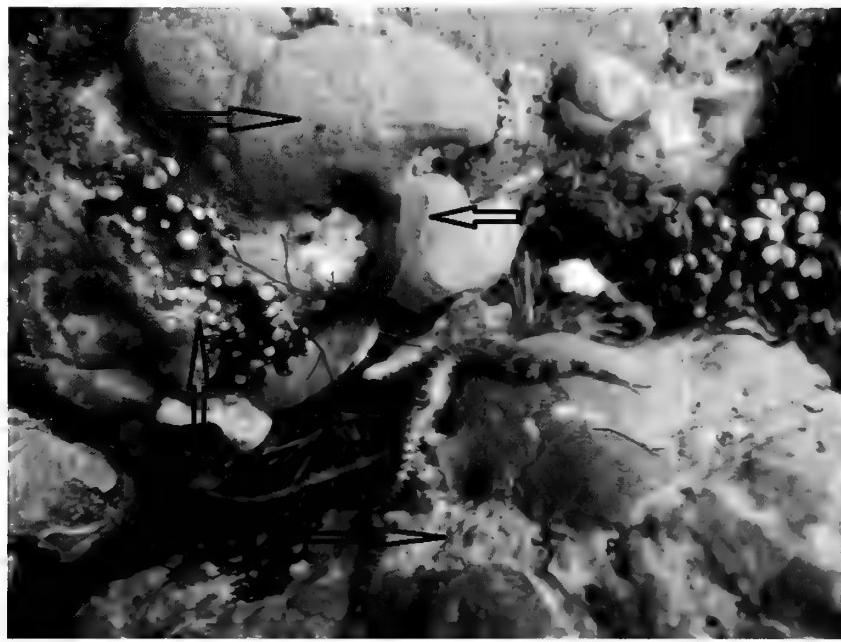


FIGURE 18. Shallow-water habitat (3–5 m), with young (estimated 60 years old), mound-forming plants of *C. compactum* in NE Newfoundland. Some plants are strongly faceted (right arrow); others are more dome-shaped without facets (top arrow). Several plants are fusing and with time will develop clathrostomes. The branching red coralline is *Lithothamnion glaciale* (left arrow). Image by Alok Mallick.

rate as a function of temperature fully explains differences in both mean yearly thickness and conceptacle maturity time for *C. compactum* from the Gulf of Maine to Labrador and for *C. nereostratum* in the North Pacific. Since detailed temporal conceptacle development data are not available for *C. nereostratum*, approximate temperature-growth curves are presented, but conceptacle development is not included on the graph. On the basis of a comparison with Gulf of Maine data, conceptacle maturation of *C. nereostratum* in the North Pacific should be similar to, but a little slower than, that of *C. compactum* in the Gulf of Maine. Field data from the Aleutian Islands are inadequate to fully verify this hypothesis.

WALL STRUCTURE AND CALCIFICATION

As demonstrated by Adey (1965) for *C. compactum* and by Lebednik (1976) for *C. nereostratum*, all perithallial growth and calcification in *Clathromorphum* occurs in the primary meristem. Herein growth and calcification are shown to occur along a narrow horizontal plane through the meristem (Figures 17, 24). With no bridging calcification (perithallium to epithallium), a fracture plane can be easily induced. Although a secondary meristem can form within broken-out conceptacles or on damaged surfaces (in the uppermost perithallium), the primary meristem produces most of the calcified tissue. As shown in Figures 16A,B, 17B,D, and 24B and unlike other genera of

corallines (Adey et al., 2005), the interfilament calcite crystals in *Clathromorphum* are larger and more irregular than the inner-wall crystals; the latter are short, prismatic, very fine, and oriented radially. The interfilament crystals are oriented vertically or diagonally and tend to be deltoid in shape. The thickness of the radial, inner-wall crystals remains largely unchanged seasonally, whereas interfilament calcification is thick in summer and absent or thin and irregular in winter. This pattern also occurs in the naturally etched surfaces of bivalve-bored cavities, where the layers form ridges in the summer and grooves in the winter (Figures 19, 20).

In decalcified sections (Figure 8E), epithallial filaments, lacking cell fusions, often disaggregate. In perithallial tissues, the filaments are mostly cohesive because of the fusions organically linking adjacent filaments. Nevertheless, between the fusions and in the cells below the meristem where fusions are lacking, filaments can locally disaggregate since there is no common interfilament wall. In the perithallium, inner calcified cell walls are organically framed, whereas the space between the filaments is apparently devoid of organic material and may or may not be filled with carbonate, depending on the season. It has been widely accepted that calcification in corallines is “simple” precipitation resulting from removal of CO₂ during photosynthesis, with organic nucleation centers specifying calcite rather than aragonite (Ries, 2010; however, see Adey, 1998). This is highly unlikely in *Clathromorphum* species of Arctic and Subarctic seas because as

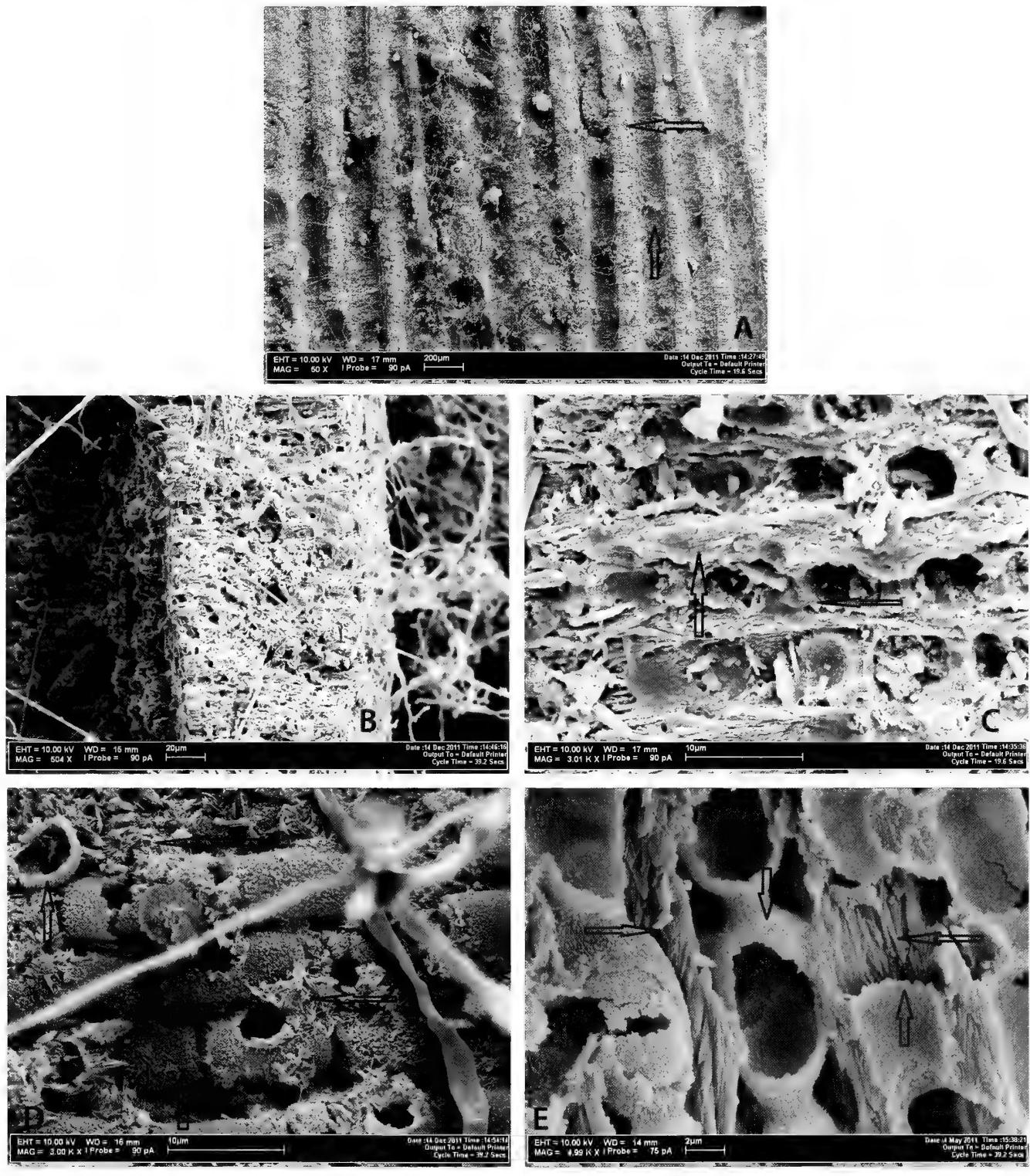


FIGURE 19. Images from *Hiatella*-etched cavities in *C. compactum* from southern Labrador. (A) Ten years of growth with ridges and valleys for each year (summer, top arrow; winter, bottom arrow). (B, C) Surface of summer-fall ridge showing dense interfilament crystals (vertical arrow) maintaining structural integrity (horizontal arrow in C shows inner radial crystals). (D) Winter valley showing the breaking out of minimal interfilament crystals (horizontal arrows) and the integrity of individual cells and their organic radial-crystal-embedded walls (vertical arrow). (E) Oblique view of the ridge side, showing the intermediate breakdown stage and the great difference between fine inner-wall crystals (vertical arrows) and large, angular interfilament crystals (horizontal arrows).

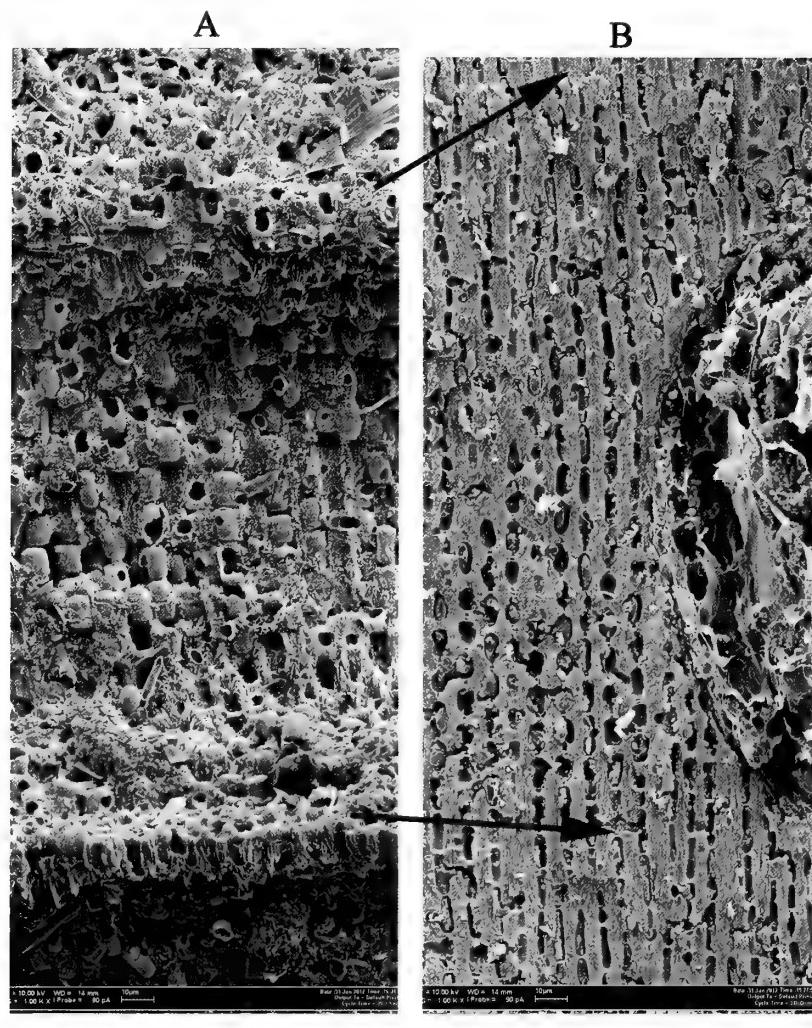


FIGURE 20. Sections of *C. compactum* from nearby stations in northern Labrador, off Nain, over a single year of growth, showing two summer bands (arrows) of dense interfilament calcification separated by a wide band of winter cells having little interfilament calcite. (A) Etched wall of a *Hiatella* cavity, 9–11 m depth at Jenks Island. (B) Vertical fracture of a plant from Baker Island, 12–14 m depth. These yearly bands are not of the same age; B shows a year with 20% more year growth than A, as arrows indicate.

has been shown (discussed further below), they can continue to grow and calcify for at least part of a sunless winter. (Laboratory studies underway also show repairs to damage of the perithallium with growth in total darkness; Adey et al., unpublished).

Moreover, in Labrador and the high Arctic, where clathrostomes lie 10–30 m deep under several meters of sea ice and snow for 6–10 months of the year, winter calcification driven directly by photosynthetic CO₂ removal seems unlikely. The pattern of inner-wall calcification remains seasonally constant, changing only in cell length and requiring only additional radially placed integral crystals of the same form. As suggested by Adey (1998), inner-wall crystals in corallines are likely nucleated

on organic templates and metabolically emplaced by ion pumps in cell membranes. If so, rather than being diffusely distributed over the length of the meristem cell and into upper perithallial cells, these carbonate additions occur in a plane in the meristem (i.e., a ring around the “middle” of each cell). On the other hand, interfilament calcite formation in northern waters, strongly tied to summer tissues, could result from precipitation as a result of photosynthetic CO₂ removal by the epithallium. This remains to be determined in laboratory studies.

Clathromorphum spp., along with many coralline genera, not only have a considerable ability to turn calcification on and off (for example, in conceptacle formation) but are also broadly

capable of dissolving already emplaced carbonate. In the conceptacle fertile cylinder, during the formation of sporangia from the meristem, carbonate is not laid down in the cell walls of intra-sporangial filaments; 100 µm away in the vegetative tissue, normal calcification continues to occur. As sporangia enlarge, they are able to dissolve a large volume of cell wall carbonate in the surrounding and underlying vegetative tissue. These decalcified tissues are crushed by the final enlargement of sporangia prior to spore formation. Later, after spores are released, the thin, empty sporangial walls become calcified (Figures 12B, 13A). Likewise, the inner walls of meristem cells and the interfilament space are (in summer) emplaced in the meristem fracture zone with carbonate; when cut off by cell division, this carbonate joins the underlying perithallium. Then, two to five cells into the perithallium, passages (fusions) are excavated out of calcified cell walls,

laterally, to join the lumina of adjacent cells. Especially in the autumn, when sporangia begin development, these fusions may extend laterally for several cells (Figure 11B). Although the number of fusions varies considerably at the autumn “break,” when sporangial formation is initiated, they are often so abundant that they develop a plane of weakness that fractures horizontally when breaking stresses are applied when creating fracture sections (Figure 11A).

Where bivalve boring (and carbonate etching) and deeply grooved sea urchin grazing occur, breaking the “seal” of living tissue over dead carbonate, alteration of carbonate chemistry is likely. These diagenetic zones have ecological signatures, often with the formation of epi- and endophytes on the dead crust. Also, in thick clathrostomes, occasional fractures develop because of wave or moving substrate stresses. Alteration of carbonate along

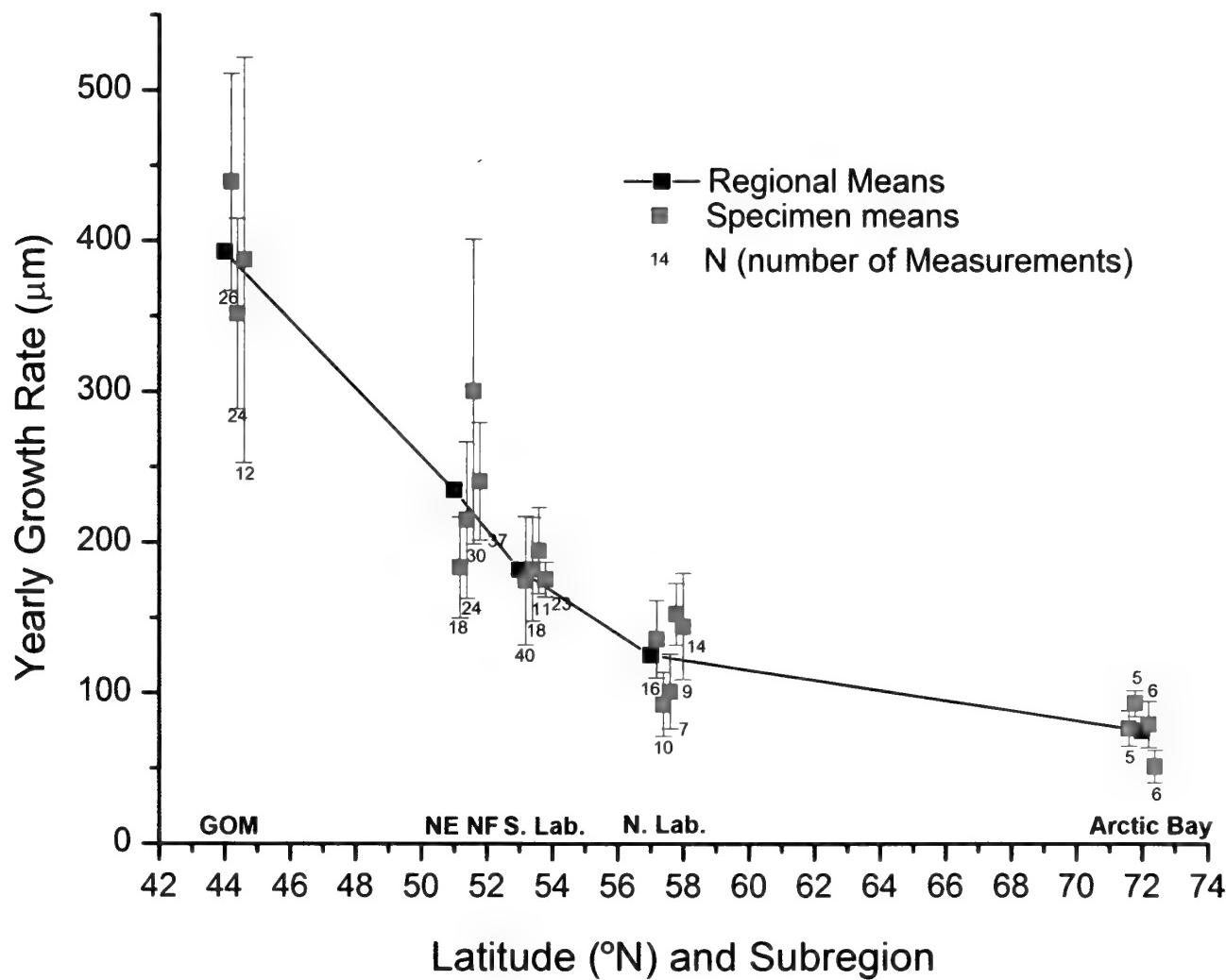


FIGURE 21. *Clathromorphum compactum*. Regional yearly crustal accretion of haphazardly selected specimens and years as a function of latitude in the northwestern North Atlantic, Labrador Sea, and Arctic Bay, northern Baffin Island. The red squares are individual specimens. In Newfoundland (NF) and Labrador, each data set included one sample from *Hiatella*-etched burrows; otherwise, data are from analyses of conceptacle layers on SEM mosaics.

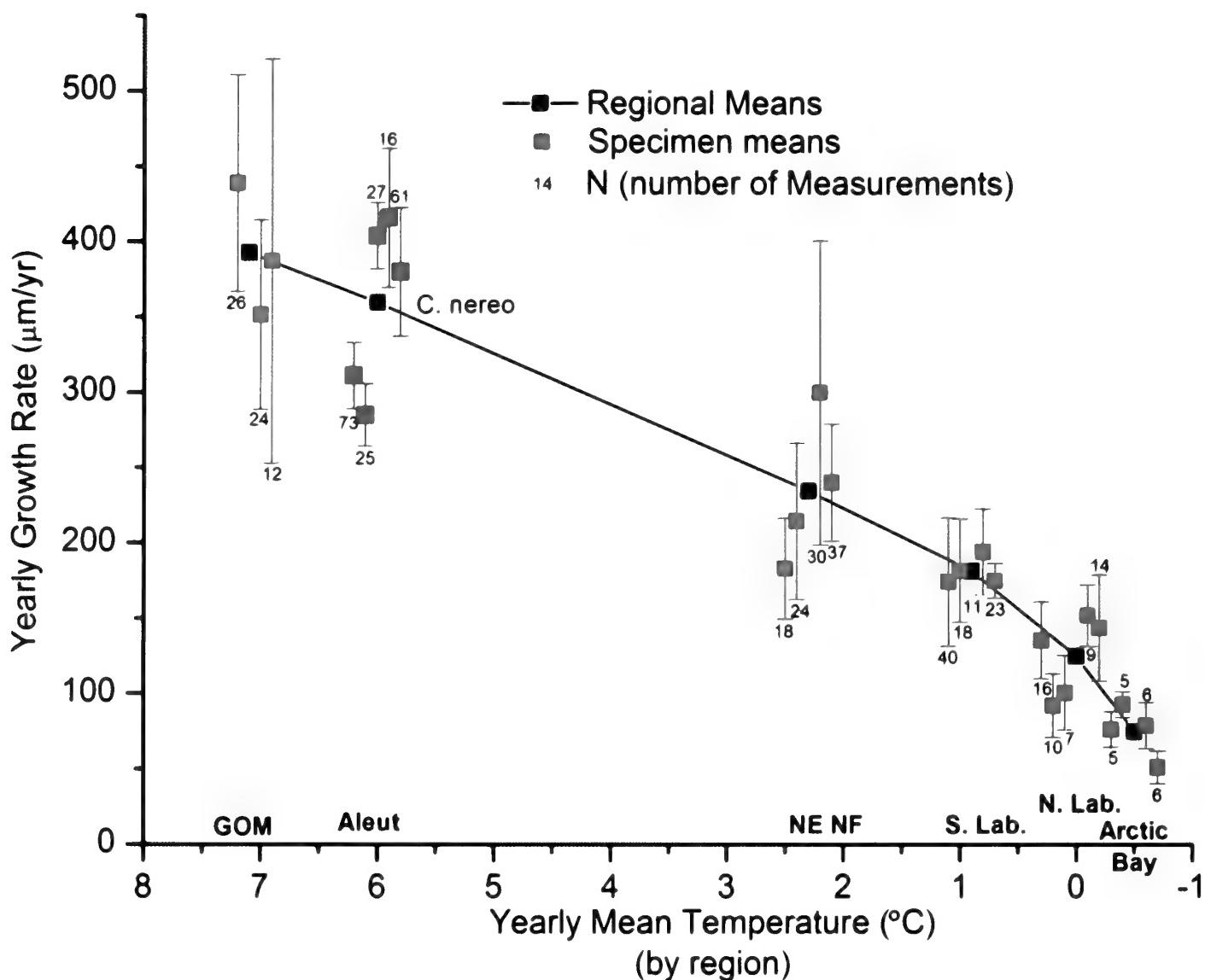


FIGURE 22. Growth rate of *C. compactum* (red) and *C. nereostratum* (blue) as a function of mean yearly ambient temperature. The regional temperature derivation is described in the Figure 23 caption. The downturn in the curve on the right is due to the length of winter sea ice (Halfar, unpublished data).

such fractures is sometimes clearly visible in SEM images. Generally, such alteration occurs only near damage sites and is easily detected and avoided. As older clathrostromes are discovered, it will be necessary to carefully examine the oldest part of the coralline carbonate for potential diagenesis.

ECOLOGY AND GEOMORPHOLOGY

The 2010–2011 cruises to Labrador demonstrated that outer coast islands can provide localized optimum conditions (Figures 2A,B, 25A,B) for the development of clathrostromes of *Clathromorphum compactum*. On the leeward sides of these islands and

especially on the more protected parts of outer coast island complexes, where wave exposure is moderated, clathrostromes are often well developed. Particularly, where stable bedrock shores have a minimum overburden of glacial till (avoiding wave tools) yet have enough wave action to seasonally limit sea urchin grazing, an optimum environment for carbonate production in *C. compactum* is present. Low-lying, domed bedrock islets lacking the high cliffy shores that could shed falling boulders and cobbles onto the underlying shore can have particularly well-developed clathrostromes. Moderately steep bottoms of cobbles and large boulders that limit downslope movement create the optimum conditions for preserving clathrostromes for many centuries.

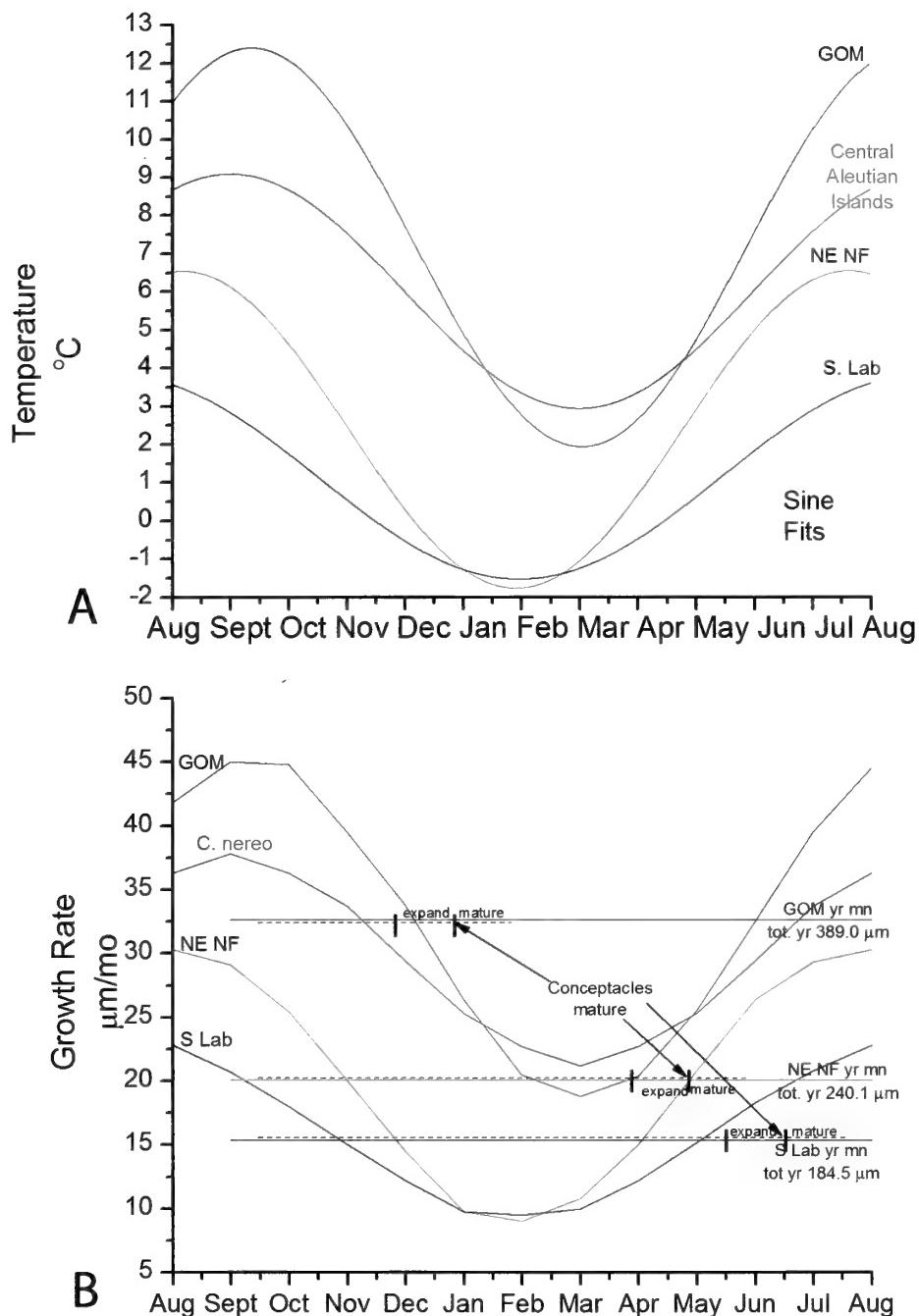


FIGURE 23. Model demonstrating regional temperature control of monthly growth in thickness and reproductive maturation in *C. compactum*, using the yearly temperature curve of Figure 22 (see text for complete description). (A) Regional temperature at 12–17 m depth for coastal waters (the Gulf of Maine from Gulf of Maine Observing System buoys, mean of Penobscot and eastern shelf buoys, 2 and 20 m, 2011 data, -1.0°C for samples from 1960s) and southern Labrador and NE Newfoundland summer data from 1964 and 2003–2011 cruises of the R/V *Alca i*, with winter estimated as -1.5°C when sea ice was present (from U.S. Navy Hydrographic Office Sailing Directions). (B) Expected regional monthly growth rates derived from the curves in A and Figure 22, summed for yearly means. The expected time of conceptacle development based on 100- μm perithallial growth to reach expansion phase and 1 month for expansion and 1 month to maturity. Dashed horizontal lines are conceptacle development time. *Clathromorphum nereostratum* curves are added for comparison, but conceptacle development is not shown (see text).

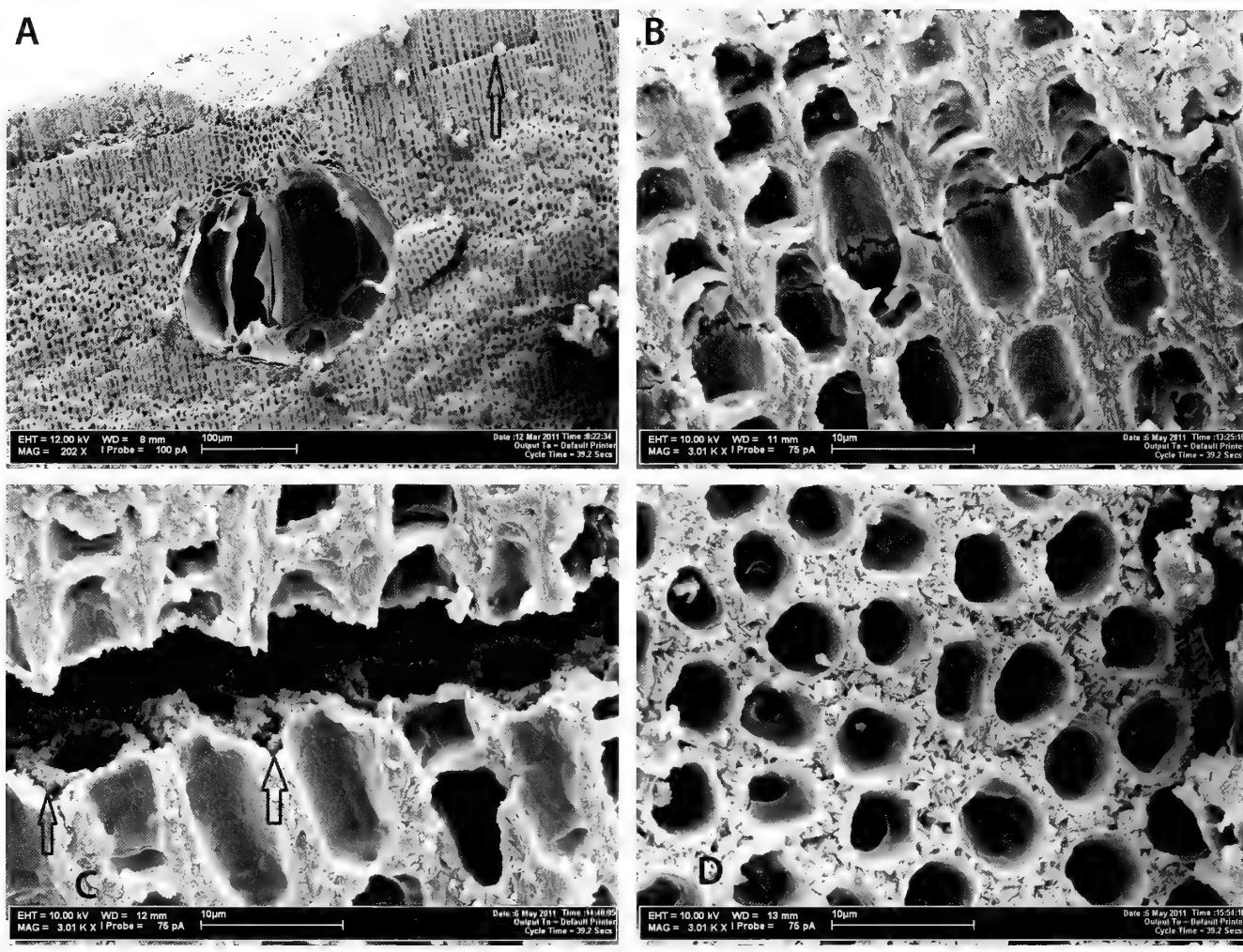


FIGURE 24. Meristem fracture and calcification zone in a specimen of *C. compactum* from southern Labrador for comparison with *C. nereostratum* (Figure 17). (A) The meristem (arrow to the right) shows fracturing in the calcification zone. The conceptacle formed the previous fall and winter, with expansion down into the previous summer band. A new meristem formed over roof but has not yet filled the depression in the epithallium (see Figure 9B). (B) Fracture zone in the meristem. (C) Fracture zone in the meristem opened up to reveal distinct interfilament grooves (precipitation cavities?) between meristem cells (arrows). (D) Meristem fracture zone (in summer) looking into the perithallium. Dense organic material covers the inner-wall crystal band, with interfilament crystals having no organic cover.

Hiatella arctica, a boring bivalve, is the chief biotic component responsible for degrading and limiting *Clathromorphum compactum* buildup in the northwestern Atlantic. *Hiatella arctica* also occurs in *C. nereostratum* in the North Pacific (Chenelot et al., 2011), but it is overshadowed by an abundance of other invertebrate infauna. *Hiatella arctica* must gain access to the *C. compactum* crust during settlement at a growing coralline margin or following sea urchin grazing or other injury. The intercalary meristem, with an epithallium subject to constant chiton grazing (and more occasionally sea urchin and limpet grazing), prevents most invertebrate and seaweed recruitment. When recruitment of several coralline species has been optimal, entirely covering a rock surface with coralline carbonate, and when sea urchin grazing is limited, *H. arctica* recruitment is minimal.

Thus, there is an inverse relationship between the success of *C. compactum* and *H. arctica*; when the factors supporting strong clathrostrome development are optimal, boring by *H. arctica* is most limited. Burial of the base of old *C. compactum* mounds by accumulating fine sediment can also create anaerobic zones that prevent further *Hiatella* boring. Under these conditions, continuous carbonate accumulations exceeding 1000 years can develop (Adey, unpublished).

Lithothamnion lemoineae, a branching coralline species, has an ecology similar to that of *Clathromorphum compactum*. Although generally less abundant, it is an integral component of northwestern Atlantic clathrostomes. *Lithothamnion lemoineae* is a particularly important component of clathrostomes in that it often “seals” the sides of *C. compactum* mounds, thereby

limiting *Hiatella* access. In the more protected bays and fjords of inner coasts, *C. compactum* is considerably less abundant and often absent. Where lower salinities and higher sedimentation are present, *Lithothamnion glaciale* becomes the dominant coralline species of northern rocky bottoms.

In the northwestern Atlantic, *Clathromorphum compactum* is most abundant, relative to other corallines, at mid-photic depths (10–20 m; Adey 1965, 1966b). We have developed a clathrostrome index utilizing the number of samples from each station depth, the mean thickness of collected samples, and the maximum single-sample thickness as an indicator of

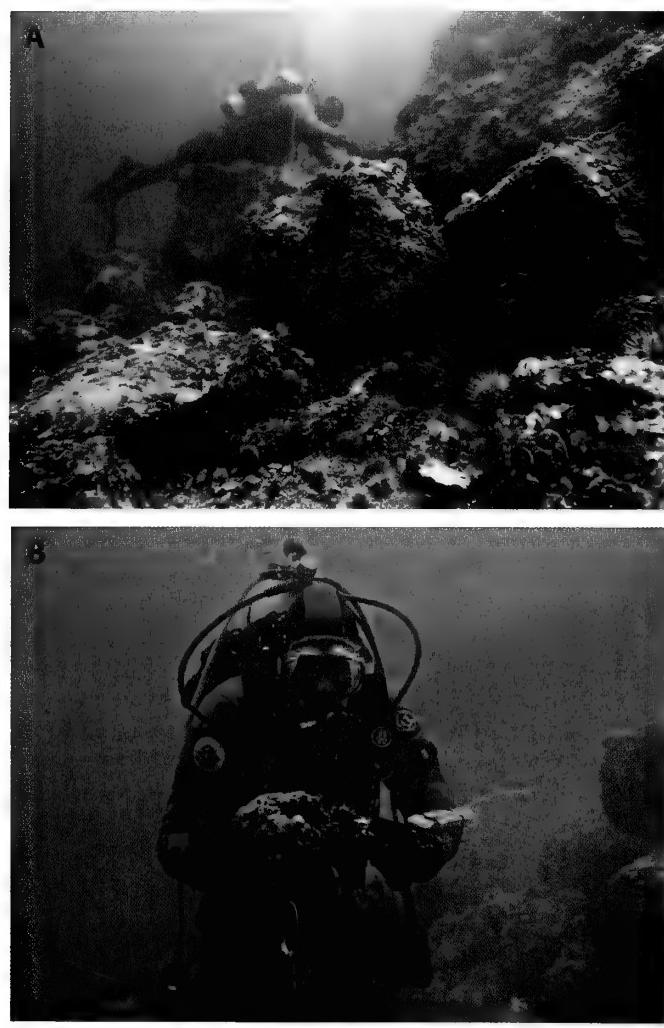


FIGURE 25. (A) Typical boulder slope on low islands in northern Labrador (at 25 m depth). Rock surfaces covered with coralline crust dominated by *C. compactum*. Large, angular, sheet-fracture-produced boulders protect glacial cobbles and small boulders from downslope movement. (B) Diver with 105-mm-thick clathrostrome extracted from the same locality. At a summer temperature of 5°C–8°C, the growth rate of this crust was about $130 \mu\text{m yr}^{-1}$, with an age exceeding 800 years.

clathrostrome development (Figure 26). Since all collections (2010–2011) were taken by a single individual and dives were of a uniform length, the number of samples (N) taken at each station depth are an indicator of the abundance of thick material. As shown in Figure 26, for southern Labrador, clathrostrome buildup also tends to peak at optimum abundance depths and at mid-wave exposures. This is generally below the shallower *Alaria* kelp zone but within the *Agarum* savanna (Adey and Hayek, 2011), from 10 to 25 m. In northeastern Newfoundland and the northern Gulf of St. Lawrence, where the water is generally more turbid, peak clathrostrome development occurs at shallower depths (5–10 m). The thickest *C. compactum* collected in the northwest North Atlantic to date were taken off Hopedale, Labrador, in the summer of 2011. Several crusts exceeding 100 mm in thickness were found.

TISSUE IRREGULARITY

Under some conditions, the perithallial tissues of *Clathromorphum compactum* and *C. nereostratum*, as produced by an essentially planar (faceted) or domed meristem, can be quite regular. However, grazing by sea urchins, death due to disease, and grow-out from damaged postmature conceptacles can change not just cellular orientation but also planar temporal variations in seasonality and therefore calcite crystal chemistry. When the meristem and upper perithallial tissue are removed by grazing or other abrasion, meristem regeneration is possible, approximately to level of the base of the most recent layer of conceptacles (200–500 μm deep). While wound tissue tends to repair these irregularities, in large part, it is this meristem regeneration on an irregular surface, rather than on a planar or domed surface, that renders archiving potentially problematic.

The most difficult scenarios for climate archiving are the removal of calcified tissue and the death of the meristem and upper perithallium to below the level at which cells are capable of meristem regeneration. In the clathrostrome environment, this “dead” surface is for a time occupied by other crustose or filamentous species of algae, boring algae, and encrusting invertebrates. Eventually, the dead surface is likely to be overgrown by new *Clathromorphum* tissue from the sides or in some cases by new spore settlement. However, several years may intervene, creating a disconformity or even an unconformity of unknown longevity. By matching several seasonal bands or patterns in adjacent perithallium or other plants or by dating, it may be possible to fill in such unconformities.

Chiton Grazing

In the northwestern North Atlantic Subarctic, chitons and limpets are prominent grazers of *Clathromorphum compactum* surfaces. Chitons, particularly the species *Tonicella rubrum*, are ubiquitous on coralline surfaces, especially those of *C. compactum*. Collected specimens of *C. compactum*, left to dry, usually reveal many small animals that were not visible at the time of

collection; these mostly nocturnal invertebrates crawl out of numerous crevices and borings in the drying crusts. The shallow, parallel, scraped groove patterns of chiton grazing are abundant and easily visible in SEM images of *C. compactum* surfaces (Figure 9). However, chitons rarely affect the regularity of carbonate buildup since they graze only the surficial part of the epithelial tissue; indeed, like grazers of grasslands, chitons are probably nearly symbiotic in their relationship to *Clathromorphum* plants, preventing settling by organisms, algal or invertebrate, that otherwise might cover the surface (Steneck, 1992).

Sea Urchin Grazing

Strongylocentrotus droebachiensis, the green sea urchin, is an often-abundant species on most shallow rocky shores in the northwestern North Atlantic. Like *Clathromorphum*, the echinoid *S. droebachiensis* is a member of a North Pacific group (the Strongylocentrotidae) and is circumboreal in distribution, North Atlantic and North Pacific. In the Bering Sea, additional species

of Strongylocentrotidae join with *S. droebachiensis*. These species are typically grazers of brown seaweeds, including *Alaria*, *Saccharina*, *Laminaria*, and *Chordaria*, where they are available. Green sea urchin grazing can be strongly limited by wave action in exposed, shallow waters, and they are known to move to deeper waters in winter to avoid the more destructive wave action common at that time of the year. Controlled by shallow-water wave action, they will aggregate into “fronts” or lines and can graze into the margins of shallow kelp beds, reducing the kelps to stubble or “barren grounds.” However, *S. droebachiensis* will actively avoid some common algae of northern Atlantic regions (e.g., *Agarum*, *Desmarestia*, *Ptilota*) because they are protected by distasteful or toxic chemical compounds. At the depths where *C. compactum* is most abundant and well-developed clathrostomes are most common, it is these protected species of fleshy algae that form the overstory; these species create a patchy “savanna” of coralline alternating with fleshy algal forests that have been mistakenly referred to as coralline-urchin barrens. *Strongylocentrotus droebachiensis*, at moderate density but with insufficient

Clathrostrome index ($N \times mn + \max$)

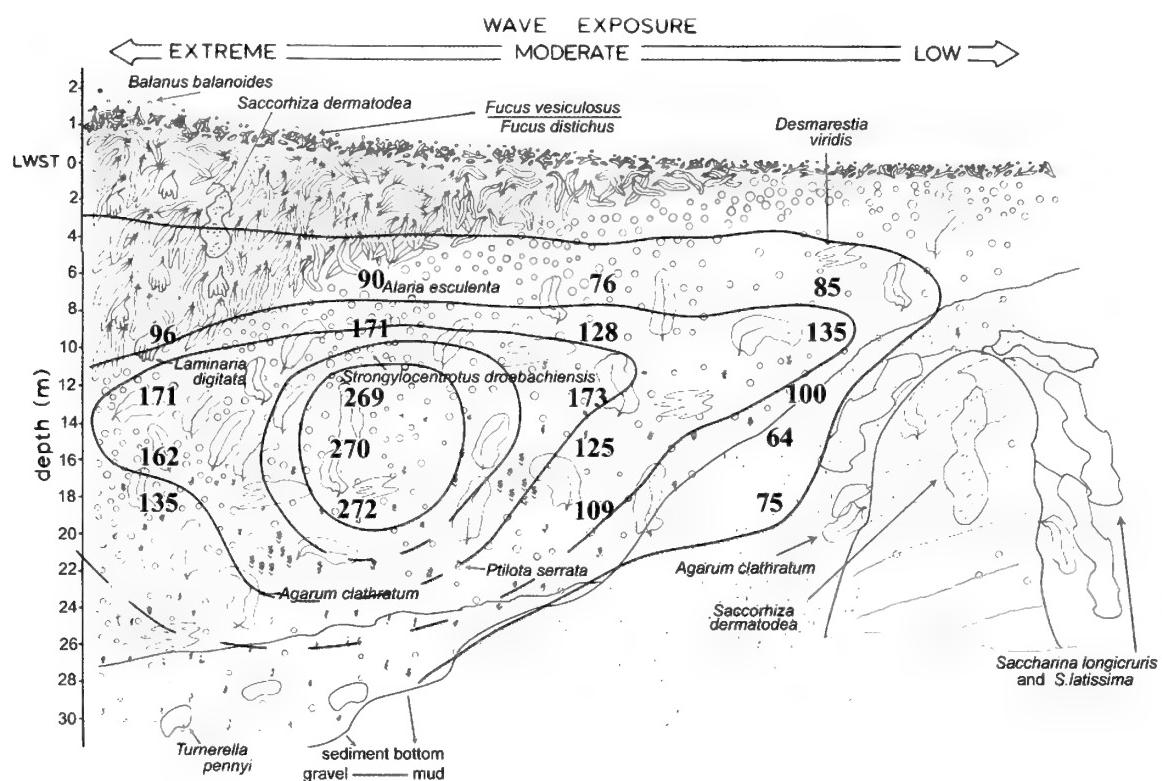


FIGURE 26. Clathrostrome index for the southern Labrador coast (see text for explanation of formula) from the 2010 cruise of the R/V *Alca i*. The base diagram is a community structure model for western Atlantic Subarctic rocky shore from Adey and Hayek (2011). Abundance and thickness of *C. compactum* crusts peak from 12 to 20 m on moderately exposed shores. LWST = low water spring tides.

algal food, can survive by severely slowing their growth and can even become reproductive on overgrazed coralline bottoms (see Adey and Hayek, 2011, for a review of this topic).

In the northwestern Atlantic, when larger fleshy algae are not available, large populations of very small green sea urchins can subsist in crevices, without growth, on diatom and filamentous algal mats (Himmelman, 1986). Coralline-dominated bottoms, including clathrostomes, usually harbor populations of young urchins that can survive for many years awaiting more favorable feeding conditions. This is an unstable situation, and although very small “standby” urchins are not likely to significantly affect the growth and anatomy of *Clathromorphum compactum*, population explosions leading to larger urchins, with transitory fleshy algae for support, can do considerable damage to *C. compactum* plants. Occasionally, adult green sea urchins will graze surfaces of *C. compactum*. Although the sea urchins typically remove only scattered patches or grooves of coralline surface that will be regenerated, this grazing can create an irregular terrain of secondary tissue. When sea urchin grazing is very extensive, reaching below the regenerative surface band, an unconformity will develop. Usually, this surface is overgrown again from the side, beginning with new basal, or hypothallial, tissue. The result can be several years of missing carbonate. Sometimes this is obvious (Figure 2B) because a layer of epiphytes and endozoic green algal borers, or even other corallines, have settled; however, if the missing periods are not recognized from SEM observations, the resulting archive can be seriously misinterpreted.

Conceptacle Breakout

Typically, during post reproduction and after spores are released, cells at the margins of the conceptacle roofs, or the roof itself, will regenerate meristem cells (Figures 9, 10, 12B). This leaves conceptacle cavities often with secondary calcification in the sporangium walls; these are quite visible and easily avoided during geochemical analysis. However, in some cases, a conceptacle roof can break out, either autonomously or because of grazing. When that happens, secondary meristems form, and new tissue from the sides and bases of the conceptacle cavities develops (Figure 12B). The accompanying cellular carbonate, although showing a minimum pattern disruption, is formed many months later than the surrounding carbonate. This can be hard to recognize without SEM examination.

Death Due to Disease

Killing disease has been documented in corallines (Littler and Littler, 1994) and has long been recognized in Subarctic waters. Typically seen as white, expanding patches with green centers (as epiphytic and endophytic algae occupy the dead crust), these patches are usually no more than a few to 10 cm in diameter. However, they can expand to a meter or more. Generally, when the patches are small, they are regrown laterally by secondary hypothallium; in the case of larger patches, resettlement probably occurs. Sometimes,

grazing by green sea urchins on the epiphytic and endophytic secondary algae in the dead patch can remove several years of *Clathromorphum* carbonate accretion. This can develop an unconformity, with new growth layers not being parallel to the pre-disruption layers; the number of missing layers would have to be documented by matching of cyclic patterns or cross dating.

DISCUSSION

We have described the patterns of growth, reproduction, and layered carbonate formation, the intricacies of calcification, and the basic ecological patterns for the most abundant Subarctic-Arctic *Clathromorphum* spp. This description provides a framework for increasing our understanding of a key element of a widespread and characteristic ecosystem and its basal biogenic carbonate component. The structure of the overlying fleshy seaweed community in the northwestern Atlantic, characterized with quantitative data and supported by many published studies of plant-animal interactions, has been summarized by Adey and Hayek (2011). Although ecological studies of the Subarctic fringe occurrence of this ecosystem in the Aleutian Islands have been published (e.g., Steneck et al., 2002; Springer and Estes, 2003; Estes et al., 2005; Trites et al., 2007; Chenelot et al., 2011), the information for the northwestern North Pacific and for *C. nereostratum* is more fragmentary. A better understanding of the autecology of *C. nereostratum* in the Aleutian Islands and the island and mainland coasts of the Bering and Okhotsk Seas is necessary.

CLIMATE ARCHIVES

The information we have presented can also provide critical support for further development of already promising Arctic-Subarctic climate archives from both *C. compactum* and *C. nereostratum*. In the skeletons of these species, there is potentially a wealth of ecological and water state (climate) information available in the complex formation of yearly layers of carbonate-encased cells and reproductive structures. Also, there is no known biological limitation, inherent in the coralline structure itself, to the preservation of the information built into the carbonate, although the high-magnesium calcite itself is relatively unstable and subject to later diagenesis. Given geographic identification of sites with the geomorphological and oceanographic conditions that produce long-term continuous accumulation of carbonate, more than a thousand years of detailed subannual ecological and climate information can be obtained. Data derived solely from anatomical features not degraded by chemical alteration (e.g., thickness of yearly bands) could extend the archive considerably further. Recovery of specimens transported to sedimentary environments could also produce records of longer duration. However, as we have described, the complexity of the *Clathromorphum* skeleton is such that considerable care needs to be taken to understand the details inherent in the anatomy of this genus if analytical variation is to be separated from environmental variation.

MECHANISMS OF CALCIFICATION

The mechanisms of calcification in *Clathromorphum* also need to be fully understood with intensive laboratory research if sources of measurement variation are to be removed from these archives. In this genus multiple calcification sites and autogenic dissolution are general capabilities of the organism. Whether secondary calcification (e.g., sporangial wall calcification) is metabolic or, as is more likely, simply carbonate chemistry in the mostly enclosed conceptacle cavity environment remains unknown. Although the precise chemistry of carbonate dissolution by both vegetative cells (fusions) and sporangia remains unknown, there is little question of its routine occurrence. This is also true for the interfilament (outer cell wall) formation of calcite crystals, although a role for light in directly controlling chemistry seems possible in this case.

As we noted in the Introduction, all coralline genera have cell walls with prismatic, high-magnesium calcite crystals inserted in the cell wall perpendicular to the cell lumen. Since cell elongation in some genera is progressive with depth in the perithallium and in many genera each filament has independent cell division and growth, cells have a very thin outer wall of flat crystals parallel to the filament axis that functions as a glide plane (Adey et al., 2005). On the other hand, two very different, concurrent mechanisms for calcification in *Clathromorphum* are distinguished in this volume. Although developed specifically on the basis of the abundant information available for *C. compactum*, there is little obvious difference found in the tissues of *C. nereostratum*. Primary calcification is likely an ion pump-driven process that forms inner cell walls that include high-magnesium calcite crystals. These crystals are embedded in an organic matrix that provides a mineralogical template. At winter temperatures (0°C to -1.8°C) on the southern Labrador Coast, cells of *C. compactum* are typically 9–10 μm long; at summer temperatures (3°C – 4°C), they are longer (12–13 μm) and have a length-based increase of inner-wall carbonate volume.

The production of new inner cell walls with calcite crystals appears to be directly controlled by temperature; the higher the temperature is, the greater the vertical extension of the organic wall is. Vertical extension (growth) occurs with crystal emplacement in the inner-wall matrix of a meristem cell, along with organic wall material. In the Labrador winter, not only is there a roughly 20% reduction in cell length, there is also an approximately 30% reduction in the number of cells produced per month. These factors are reflected in the 60% reduction in yearly growth from the south northward on the North American coast and a further 75% reduction continuing northward to northern Baffin Island (Figures 21, 22). The thickness of inner cell walls, with their embedded prismatic calcite crystals being radially oriented and less than a micron in length, is constant with temperature, light, and time. It would appear that *Clathromorphum* species and perhaps crustose corallines in general have “boxed” themselves into a carbonate framework that is limited by temperature control of metabolic calcite crystal emplacement and not by potential productivity. If the growth curve of Figure 22 is extended

to a tropical temperature of 25°C , yearly accretion would be 1–2 mm yr^{-1} , approximately the rate of algal ridge accretion in the Caribbean by *Porolithon pachydermum* (Adey, 1978).

Except for a few obligate parasites, crustose corallines are photoautotrophs with plastids, chlorophyll *a*, and phycobiliprotein pigments; photosynthesis is required at least at some point in a plant’s life cycle. Whereas Adey (1998) had presented a model for crustose coralline calcification that is driven by ion pumps, some recent researchers (Ries, 2010) have suggested that all calcification in corallines is directly driven by the photosynthetic removal of CO_2 followed by a corresponding pH increase and chemical precipitation. The calcified tropical green algae *Halimeda* is a well-published model for CO_2 removal-induced aragonite formation in enclosed algal tissues. However, as we have described, at least in *Clathromorphum*, where winter growth in Arctic darkness and additionally beneath sea ice is a significant part of total calcification, the formation of high-magnesium calcite crystals must be metabolically driven using stored photosynthate.

Precipitation might be the dominant form of calcification in non melobesiod tropical genera of corallines, which have been the subject of most calcification research. However, a survey of high-magnification SEM scans of several tropical genera has shown that inner-wall calcification morphology is quite similar to that described here. It is likely that other Arctic-Subarctic genera (e.g., *Lithothamnion* and *Leptophytum*), which lack significant interfilament calcification (see Adey et al., 2005), also calcify metabolically, not only during the dark of Arctic winters but also year-round.

PRIMARY PRODUCTION AND GROWTH RATES

Crustose corallines, particularly at higher latitudes, are very low-level primary producers (Adey, 1970, 1973) and commonly are the deepest abundant algae at all latitudes. In laboratory experiments, *Clathromorphum circumscripum*, an intertidal and shallow sublittoral plant, demonstrated a compensation point of 35 lux at 0.3°C ; at the highest temperatures usually encountered by this species (10°C – 16°C), the compensation point was 200–300 lux. In the same experiments, the deeper-water Subarctic *Leptophytum* leave showed compensation points at optimum growth temperatures (5°C – 12°C) of 35 lux. Both *C. compactum* and *C. nereostratum* are mid-depth species. It is likely that the compensation points at the temperatures that both of these species encounter range from approximately 10 to 50 lux. As we demonstrated above, the growth rate of *C. compactum* in the northwestern Atlantic ranged from roughly 100 to 400 $\mu\text{m yr}^{-1}$ latitudinally; our analysis suggests a direct relationship with temperature. One could argue that light could also be a factor over that north-south range. However, Gulf of Maine waters are highly turbid because of tidal mixing; also, in the years that WHA collected the Gulf of Maine samples from which the growth data were extracted, *Saccharina* kelp was abundant in most *C. compactum* habitats. In contrast, the Labrador *C. compactum* samples used for growth analysis were taken from very clear waters, with near-tropical visibilities, and from savanna-like habitats of

Agarum clathratum (Adey and Hayek, 2011), with mostly open *C. compactum* terrain. Laboratory experiments to confirm this analysis are now underway; however, it seems unlikely that light variation is a significant direct growth rate factor in the mid-depth range of *C. compactum* and *C. nereostratum*.

There is no anatomic or reproductive indication that growth in *C. compactum* ceases during low temperatures. Growth experiments currently underway have shown at least short term growth in total darkness at 2°C. Also, growth curves suggest that under the null light conditions below sea ice in northern winters growth continues for a short period. Figure 27 shows a 10-year mean plot of molar Mg/Ca in four *C. compactum* crusts collected off Quirpon in northernmost Newfoundland. These data were derived from equally spaced points in vertical sections. Here sea ice usually arrives along the coast in late January and remains until sometime in early April, when temperatures are near or below -1°C (Figure 23). The cold and warm peaks are virtually symmetrical, both occurring at midlevels of solar radiation, making this a temperature proxy with little direct light component. Farther north in northern Labrador and Baffin Island, these curves are quite asymmetric, suggesting that with much longer sea ice intervals (December–June), growth stops because of a lack of sufficient stored photosynthate.

INTERFILAMENT CALCIFICATION

The large and coarse interfilament (outer wall) crystals appear to be growing downward (perithallium) and upward (epithallium) from the fracture plane between meristem cells (Figure 28). It seems likely that these crystals are precipitated in the small cavities that ring each filament in the meristem calcification zone, perhaps because of removal of CO₂ by the overlying photosynthetic epithallium. From decalcified paraffin sections and SEM imaging of the meristem fracture zone, it seems likely that no organic material is present in this interfilament area. This process could involve a secondary mechanism of ion pumps delivering calcium ions to and removing hydrogen ions from the interfilament spaces of the fracture zones. However, the meristem fracture plane is directly below the primary photosynthetic tissue of these plants (epithallium), and the overlying carbonate (within the epithallium) appears to be made up of large, but thin, vertical sheets that likely provide a quite porous connection to the water at the surface of the plant. Also, in the Labrador Sea, the perithallium interfilament crystals are only formed during summer in any significant quantity. Thus, the interfilament wall component could represent the CO₂ removal and carbonate formation suggested by Ries (2011).

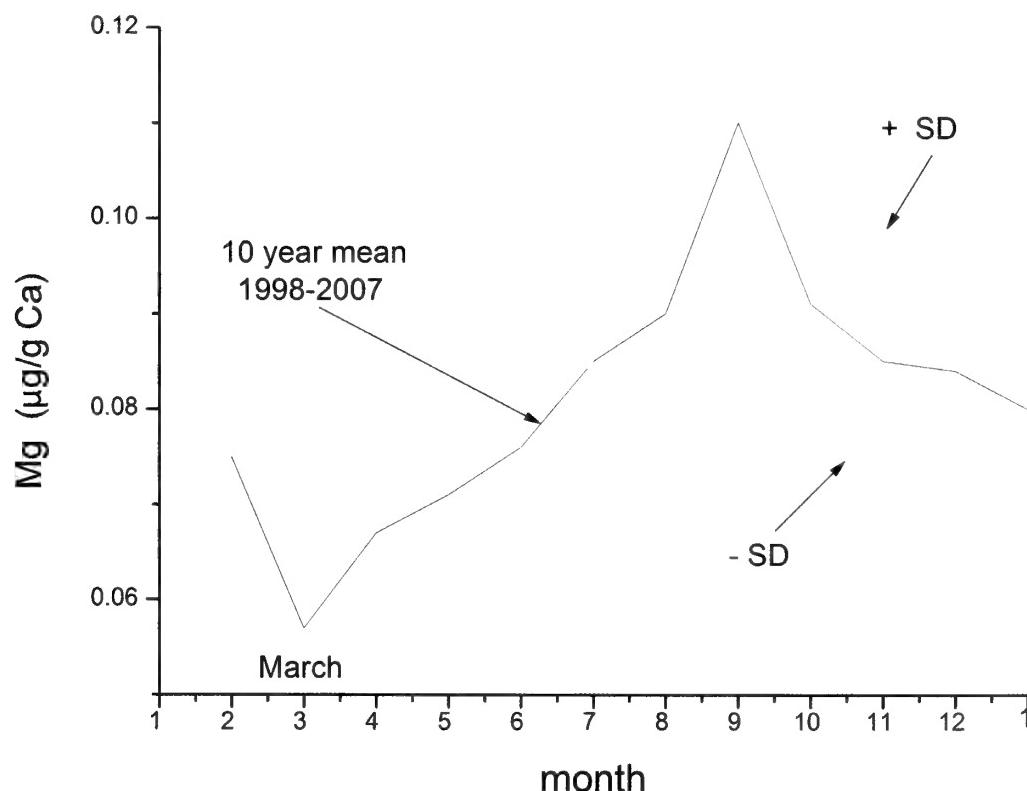


FIGURE 27. Ten-year mean molar Mg/Ca from four *C. compactum* specimens taken off Quirpon, northern Newfoundland (sample QP4-3; see text). See curves for the Mg/Ca molar ratio (proxy for temperature) in Figure 3.

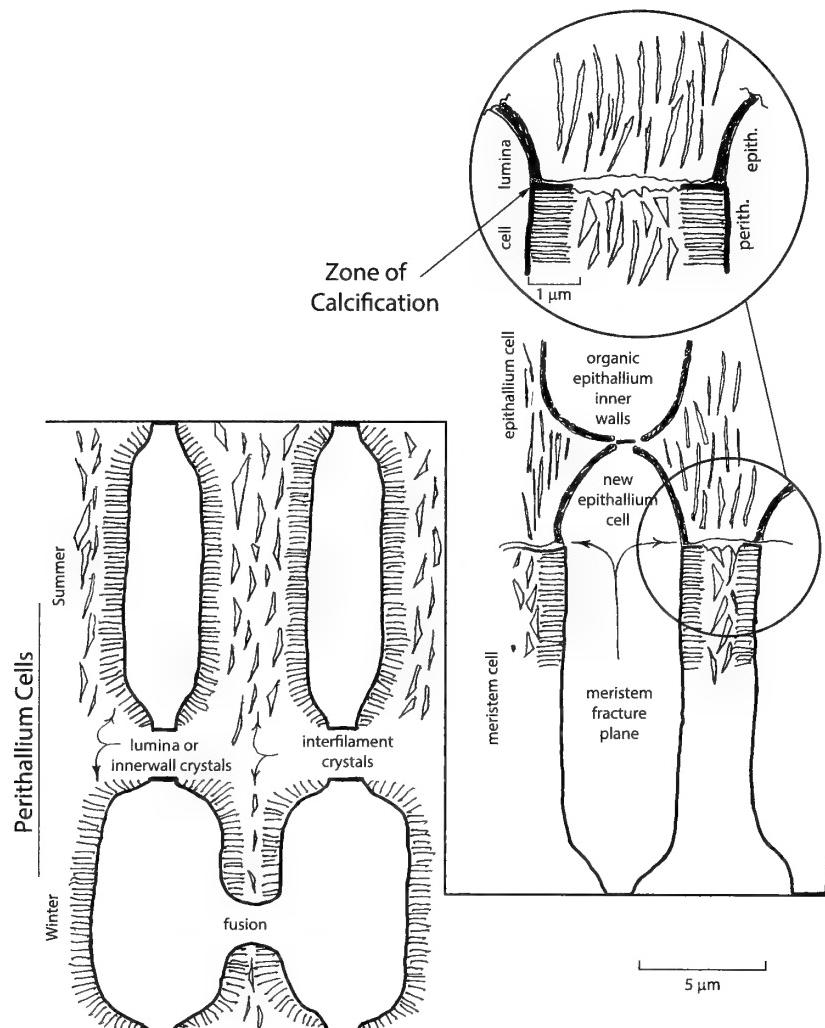


FIGURE 28. Working model of calcification in *C. compactum*. Inner-wall crystals (short, prismatic crystals perpendicular to the filament axis) form in the meristem (fracture) plane within an organic matrix and form year-round at the same dimensions; increasing numbers of calcite crystals and their organic matrix (longer cells) and production of a greater number of cells produce increased growth. Note the organic wall extending across the inner-wall crystal zone but not extending into interfilament space. Interfilament crystals (large, angular crystals parallel or diagonal to filament axes) formed, primarily in summer, in nonorganic space between filaments. Interfilament crystals extend upward into the epithallium and are thinner and flatter.

The seasonal formation of these crystals, narrows the cell lumina (since the inner-wall crystals remain the same length), and typically creates the summer high carbonate density and characteristic seasonal banding obvious in many *Clathromorphum* plants. However, development of this banding, which is partly dependent upon available sunlight, is complex. In the southernmost locality known for *C. compactum* in the Gulf of Maine, where sunlight is present in winter, seasonal banding tends to be weak because some interfilament crystals form year-round. In northern Newfoundland, with less winter sunlight, the banding tends to be more pronounced. However, in the western Labrador Sea, where sea ice forms in midwinter and remains through a large part of the spring,

the return of sunlight is greatly delayed, and the summer band of high density is very narrow (Figure 20). On the other hand, in deeper water in the same region, at the lower extent of the *C. compactum* range, peak summer temperature and maximum growth occurs in October, whereas light peaks earlier in June, at nearly the minimum water temperature. Thus, whereas high carbonate density corresponds approximately to high growth rates and long, narrow cells over most of the range of both *Clathromorphum* species, under some environmental conditions, the reverse occurs, with maximum density (due to interfilament formation) coinciding with short cells formed under low temperature. In the Aleutian Islands, *C. nereostratum* often has very strong seasonal banding,

presumably related to the intense storminess and heavy cloud cover of late winter and spring.

One of the difficulties of potentially mapping yearly layers solely from changes in carbonate density (due to interfilament crystallization that is directly photosynthesis driven) is that interfilament crystallization is directly responsive to the light regime. Although light tends to parallel temperature, ecological variation in the availability of light is extensive; perhaps more critical, shading by sea ice and snow cover on the Labrador Coast and farther north greatly delays the return of light in the spring. Although the winter temperature in shore waters at 10–20 m is little different from northern Labrador (0°C to –1.8°C) to the Gulf of Maine (0°C–1°C), the winter solar radiation under the sea ice in northern regions is nil and is greatly reduced until at least May, whereas in the Gulf of Maine and the Aleutian Islands, solar radiation is considerable throughout the winter. In southern Labrador, in shallow water (8–12 m), the period of significant interfilament crystallization is mid-May through mid-September.

CONCEPTACLE-BASED GROWTH ANALYSES

As shown in Figures 2B and 12B, reproduction, especially in *C. compactum*, can be patchy in time and space, limiting the use of simple conceptacle-based analyses in archiving. Also, damage to and even loss of yearly perithallial tissue from urchin grazing and other physical factors commonly disrupts simple seasonal layering. However, SEM imaging and mapping, accompanied by SEM-matched microprobe analysis, not only solves this problem but concurrently increases ecological and climatic discrimination. Laser ablation-inductively coupled plasma–mass spectrometry (LA-ICP-MS) has been successfully employed on *C. compactum* and *C. nereostratum* to detect changes in Mg/Ca (for temperature) and Ba/Ca (for salinity; Gamboa et al., 2010; Chan et al., 2011; Hetzinger et al., 2011), although with considerable unidentified variability (Figure 3; Gamboa et al., 2010; Williams et al., unpublished). Kamenos et al. (2008) have employed microprobe and LA-ICP-MS methods for identifying Mg/Ca variation with time, and herein extensive SEM imaging has identified structural and reproductive complexities. It seems likely that SEM mapping of laser tracks, with parallel microprobe sensing wherever anatomical complexities appear, could resolve most of the variation inherent in plant structure. This would require specimen manipulation (e.g., back-to-back analysis) since geochemical methods require polished surfaces that prevent detailed SEM analyses.

Finally, although *Clathromorphum compactum* is primarily an outer coast rather than a bay species, ecological and oceanographic variation in temperature and salinity along the complex rocky shores frequented by *C. compactum* is a widespread and inevitable source of variation. It is essential for accurate environmental archiving that multiple samples from known depths and localities be secured for analysis. The value of *C. compactum* as a millennial climate archive will also likely be enhanced by lesser growth rates in the lower SST of northern Labrador and the high Arctic. *Clathromorphum compactum* occurs throughout the

Arctic (Figure 29), and it is likely that this species can provide a pan-Arctic climate archive of considerable significance. High Arctic reconnaissance, collection, and study will need to be undertaken to fully understand the extent of clathrostrome formation.

CHANGING OCEAN pH

In the last decade, ocean acidification, resulting from increasing CO₂ diffusion from the atmosphere, has been recognized as a potential problem limiting organism calcification. Aragonite formation and high-magnesium calcite, where the magnesium concentration exceeds about 12 mol %, are susceptible to reductions in rates of formation and increase in rates of dissolution (Morse et al., 2006; Anderson et al., 2008) at lower pH. The seasonal MgCO₃ range in *C. compactum* in the southern Labrador Sea is about 6–12 mol %, and therefore, the effects of reduced carbonate saturation on cor-stromes may be minimal. In tropical waters, where magnesium content is much higher, this may be an issue of concern (however, see Nash et al., 2013).

Primary *C. compactum* calcification is metabolic, and as we have discussed, the organism maintains significant physiological control over both placement and dissolution of carbonate. Decreased pH might reduce secondary interfilament precipitation (and therefore skeletal density of summer growth). However, secondary calcification takes place internally, within highly photosynthetic tissues; it is light that limits skeletal density, and how much of a role ambient water pH plays is uncertain (Roleda et al., 2012). Chan et al. (unpublished) did not find a significant decrease in *Clathromorphum* calcification rates in recent decades in the North Pacific.

The primary function of the calcium carbonate in corallines is grazing protection. There are competing, noncalcified red species that form crusts and are more or less abundant, but usually not dominant, in Labrador Sea clathrostomes. These species and the dominant macroalgae of the community (*Agarum clathratum*, *Desmarestia viridis*, and *Ptilota serrata*) probably possess protective chemicals (Adey and Hayek, 2011). Perhaps lower pH levels could shift the balance between competing crusts, so that the noncalcified crusts would become dominant, greatly limiting development of clathrostrome structure and secondary production.

Grazers are abundant on clathrostome bottoms. Limpets and chitons have a mutualistic relationship with *C. compactum*, feeding on epithallial cells and epiphytes; not only do they rarely impact the crusts on which they feed, but they likely enhance productivity by preventing abundant algal and invertebrate epiphytism. Epithallium calcification is quite “chalky,” probably as a result of minimal inner-wall carbonate and the more “leafy” interfilament calcification. Reduced calcification might increase grazing depth, eventually reaching the meristem and causing reduced growth. However, in the short term, increased grazing depth could remove additional decaying epithallial cells and increase photosynthesis and secondary calcification. Sea urchins can significantly damage coralline surfaces and primary calcification. However, adult sea urchins do not target corallines, and



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FIGURE 29. Cor-strome, with abundant *C. compactum*, from 10–20 m in Arctic Bay in northernmost Baffin Island (73°N). These plants are growing in an inner-bay environment, not the optimum habitat for this species. Although only a single image, it suggests that extensive clathrostrome development in intermediate-exposure, island-complex environments is likely in the high Arctic. © Nick Caloyianis. Reprinted with permission.

if fleshy algae production were to be enhanced in a more acidic sea, sea urchin grazing on corallines might actually be reduced because of greater access to preferred seaweed foods. Finally, most significant grazers in clathrostrome environments also have critical carbonate hard parts that could be impacted by increased seawater acidity. Ocean acidification will certainly impact benthic communities, but the changes will be hard to predict without extensive ecosystem level experiments. Single-species studies are inadequate to the task.

CONCLUSIONS

Calcified encrusting coralline algae have a considerably more complex anatomical structure than a reading of current literature would suggest. As we document here, the genus *Clathromorphum*, widespread in Subarctic and Arctic seas, provides a highly

integrated anatomy and reproduction, modified by numerous environmental elements. Understanding this complexity is essential to the accurate interpretation of geochemical analyses of the skeleton and has already led to the development of a new archive for sea ice providing paleoclimatic information not previously available.

Also, the role of corallines in general, and keystone *Clathromorphum* species in particular, in forming cold-water rocky-bottom carbonates has been widely interpreted as a degraded ecosystem resulting from intensive overfishing. As we show, *Clathromorphum* species grow very slowly, primarily under temperature control, and have developed anatomical and cellular structures that potentially allow longevities of many centuries. This understanding is crucial to interpreting the ecological importance of this widespread carbonate structure, with its unique associations of organisms as a key ecosystem of Subarctic and Arctic rocky shores; its age shows clearly that it is not a degraded system. Also, we show how understanding geomorphological

controls laid on ecological patterns identifies carbonate build-ups, potentially of millennial ages, which are further crucial to acquiring lengthy paleoclimatic data.

Finally, contrary to the prevailing view of corallines as simple cushions built by filaments, we show how multiple complex anatomical features, which can be called tissues, and reproductive structures of combined tissues, which can be interpreted as organs, are the norm. These are key elements to understanding phylogenetic analyses and evolutionary patterns in corallines and other red algae.

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